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OTHER VOLUMES IN PREPARATION FOR EARLY PUBLICATION

The Origin of the Earth. By THOMAS C. CHAMBERLIN, Head of the Department of Geology in the University of Chicago.

The Isolation and Measurement of the Electron. By ROBERT ANDREWS MILLIKAN, Professor of Physics in the University of Chicago.

Finite Collineation Groups. By HANS F. BLICHFELDT, Professor of Mathematics in Leland Stanford Junior University.

OTHER VOLUMES PLANNED AND IN PREPARATION

The Evolution of Reptiles. By SAMUEL WENDELL WILLISTON.

Food Poisoning. By EDWIN OAKES JORDAN.

The Problem of Individuality in Organisms. By CHARLES MANNING CHILD.

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The Rigidity of the Earth and of Materials. By ALBERT A. MICHELSON.

The Problem of Fertilization. By FRANK R. LILLIE.

Linear Integral Equations in General Analysis. By ELIAKIM HASTINGS MOORE.

HEREDITY OF TYPES OF INFLORESCENCE AND FRUITS IN TOMATO.

By M. B. CRANE.

John Innes Horticultural Institution.

INTRODUCTION.

THE primary object of the following investigations in tomatoes was the elucidation of the mode of the inheritance of the forms of the inflorescence. Observations were also made on the inheritance of fruit-shape and other characters, and the results are included in this paper.

Originally two types of inflorescence were employed, but although they are widely different, it is not easy to give a clear morphological description of them, owing to their complex nature.

All the plants grown in these experiments were raised from one original cross, namely Wonder of Italy ♀ × Lister's Prolific ♂: both these varieties have been cultivated in this country for many years, and they differ considerably in several characters.

Most of the breeding was carried out under strict conditions in a house especially constructed for plant-breeding, insects being excluded.

The parent plants of a few of the F_3 families were however grown in the open, but as is explained later in this paper, the flower of the tomato is not adapted to cross-pollination. In all cases the families in question were constant to recessive characters, and individuals which proved to be of the same genetic constitution gave results analogous to those obtained in the breeding-house.

It is a general practice in the cultivation of tomatoes to remove all axillary growth from the plants at an early stage, and it was necessary to adhere to this practice with the majority of the plants grown in these experiments. A few individuals in various families were however allowed to develop naturally, so that observations might be made on the general branching system of the plants.

DESCRIPTION OF TYPES.   VAR. "WONDER OF ITALY."

Inflorescence.

The inflorescence of this variety is large and much branched; the primary branching appears to be dichotomous[1]. Subsequently much secondary growth develops and continues indefinitely. Under natural conditions the vegetative period is very long[2], and a mass of growth is formed about three or four feet wide, accompanied with fruit and flowers in practically all stages of development. (Plate I, fig. 1, ♀, and Plate II, figs. 3 and 4, $\frac{1}{11}$.) At the commencement of these experiments this type of inflorescence was referred to as "*compound*," owing to its complex nature, and it will be convenient to use this term throughout the paper.

In tomatoes the inflorescence terminates the main axis of the plant, and in these compound types this fact is evident, as the inflorescence is completely adnate throughout the axis, and does not break away from an internode of the apparent main growth. In this type the inflorescence appears to break away opposite to a *node*. Frequently however it is fused to the axillary growth for a considerable distance (Plate V, fig. 11), but as the plants get older this fusion is not so apparent, and then the inflorescence appears to arise from an internode. After the formation of an inflorescence axillary growth develops from the adjacent node. This growth usually develops six nodes and then terminates again in an inflorescence[3]. This occurrence is not however constant, and there are also cases, apparently due to displacements, where the adnation of the inflorescence referred to is not complete, but both arrangements are very regular.

[1] The branching is really false dichotomy.

[2] Plants with this type of inflorescence are not widely grown in this country, but under cultivation the practice is to remove the secondary growth from the inflorescence at an early stage, so that the primary fruits are subjected to a more favourable development. The inflorescence is therefore much smaller and the vegetative period is also relatively shorter than when the plant grows without interference. Since these experiments were commenced Messrs Buck, Nurserymen, Ipswich, have introduced a variety of tomato with a compound type of inflorescence, under the name of "Buck's Tresco." The origin of this variety I have no knowledge of, but it and "Wonder of Italy" are the only varieties, that I am aware of, that have the above described compound type of inflorescence.

[3] In tomatoes apparently a one-third phyllotaxis exists, and in these compound types an inflorescence forms at the termination of two genetic spirals.

Fruit.

The fruit of this variety is small and elongated, it has one simple division forming two cells (bilocular); many hundreds of fruits have been examined, and the above characters have been found quite constant.

B, branch.　　P, petiole,　　F, inflorescence.
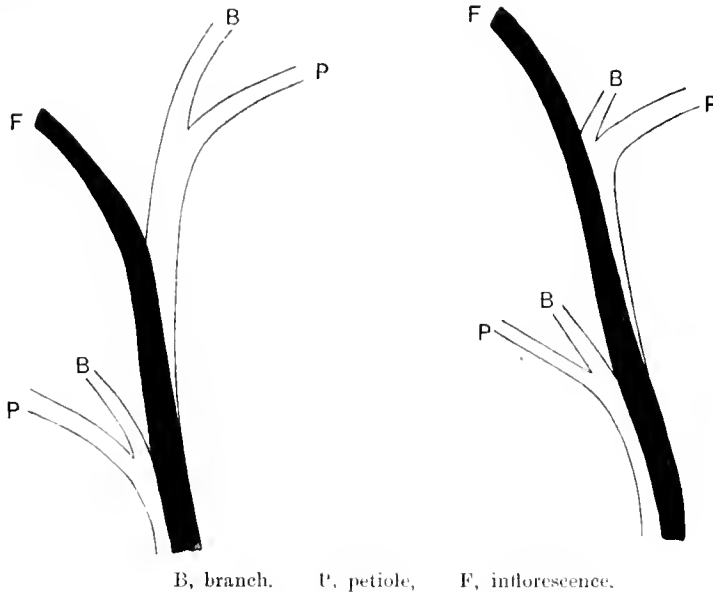
Fig. A.　"Simple" inflorescence.　　　　Fig. B.　"Compound" inflorescence.

VAR. "LISTER'S PROLIFIC."

Inflorescence.

In this variety the inflorescence is of a simple type, consisting of about nine flowers. Occasionally a solitary growth develops, but this is a rare occurrence. In contrast to the compound type, this inflorescence will be termed "*simple*."

In this type only three nodes occur (one genetic spiral) between the inflorescences, and the latter are not adnate (as the compound types are as far as the node), but break away in the *internode*. The primary growth therefore appears to be the main growth throughout the plant; but the absence of axillary growth at the node immediately above the inflorescence, shows that the leading growth is morphologically lateral as it is in the compound type. (Text-fig. A.) The above characters are not absolutely constant, but they are both very regular.

Fruit.

The fruit is round and many-celled (plurilocular), but there is considerable variation in both these characters. Occasional fruits have only two cells, and are then inclined to be conical in shape. Some have three cells, and then are mostly of a spherical shape. The fruits with the greater number of cells are more flattened in shape than those with less. This association of shape with the number of loculi is very marked in some types of tomatoes, and it is discussed later in this paper.

F_1.

Sixteen F_1 plants were grown, and they were very uniform; the simple type of inflorescence behaved as a complete dominant, as also did the characters of the ♂ parent, namely the internodal position of the inflorescences and the occurrence of only three nodes between them, but, as will be shown later, these various characters are in reality expressions of one structural peculiarity. In fifteen plants these characters were quite constant, and only one exception occurred in the remaining plant.

Fruit.

The plants matured about fifty fruits each; they were uniformly conical[1] in shape (Fig. 2). It should however be noted that although conical-shape is uniformly dominant it is not completely so, as occasional fruits, about five per cent., were round.

The fruits were predominantly bilocular[2], but occasional fruits (those which were round) were three and a few four-celled.

F_2.

103 F_2 plants were grown. 84 were the simple type of inflorescence and 19 compound type. The recessive numbers are low, but I do not think the deficiency is of any significance.

53 of the above plants were grown in 1913; 41 of them were simple and 12 compound, a fairly close approximation to a 3 : 1 ratio.

50 were grown in the following year; 43 were simple and only 7 compound.

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[1] Salaman (3) found certain differences in the shape of the berries of potatoes to be due to a single pair of factors, and that the dominant form was heart-shaped. Round × long gave a heart-shape F_1.

[2] Messrs Price and Drinkard (2), found that the bilocular character behaves as a simple dominant to the plurilocular type, but I think the plurilocular type used by them was not that of Lister's Prolific, but the *ab* type in family 1⅔.

The plants raised both years were from seeds from the same fruits grown in 1912, and it is conceivable that the seeds which produce the compound types may lose their vitality earlier than the simple type. It is interesting however to note that out of 20 F_3 families raised only two small families (29 plants) were heterozygous for compound inflorescence, and 24 were simple and 5 compound.

The compound inflorescence types are very distinct from the simple, but there is considerable variation in them, some being much larger and develop much more foliage than others, but the primary dichotomous branching system is common in all.

Fruit.

The shape of the fruit of 102 plants was recorded. They may be divided into three primary forms—conical, round and long. All these however can be further subdivided as: conical and pointed conical (heart-shape), spherical round and compressed round, full longs and pyriform long (longs with a constriction at the proximal end), etc.

The analysis of shape is a difficult problem, especially with allied forms, and undoubtedly many factors are concerned in the shape of the fruit. The family was not sufficiently large to justify the classification of all the various forms. If however length alone is taken, definite results appear to be obtained from this family; by classing the various forms of conical and round as *short*, and the full and pyriform longs as *long*, we obtain approximately a $3:1$ ratio, the longs being recessive[1]. The numbers obtained are:

	Short	Long
	78 (conical + round)	24
Expectation	76·5	25·5

Although short and long fruits and simple and compound inflorescence both behave as unit characters, the long fruit and compound type of inflorescence being the recessives, the proportions recorded were not normal, as there is a considerable divergence from the usual $9:3:3:1$ ratio. The two small F_3 families, which were heterozygous for the inflorescence, were also heterozygous for fruit shape. If we combine them with the F_2 the results are as follows (A representing the factor for the simple type of inflorescence, and B the factor for short fruit):

	AB	Ab	aB	ab
Actual numbers	91 :	16 :	11 :	13
Expectation of 9 : 3 : 3 : 1 ratio	73·62 :	24·54 :	24·54 :	8·18

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[1] There appeared in two F_3 families a distinct flattened round, which is apparently recessive to long.

The results suggest that partial coupling occurs between the factor for simple inflorescence and that for short fruit, but the numbers are not sufficiently large to form any conclusion as to the intensity of the coupling, nor to establish the existence of the same with certainty.

F_3.

In F_3 182 plants were grown from parents with the compound type of inflorescence, and they were all constant to the compound type.

The apparent position of 254 inflorescences borne by these plants and the number of nodes that occurred between them were recorded. In 227 the adnation was complete, as in the Text-fig. B, and the remaining 27 were either fused to the axillary growth beyond, or displaced. There was more irregularity in the number of nodes that occurred between the inflorescences: in 12 cases less than six nodes occurred, and in 24 more than six; in the remaining 191 cases the usual six nodes occurred.

The number of nodes and the position of 611 inflorescences on plants with the simple type of inflorescence were also recorded. 554 were constant, breaking away at an internode as Text-fig. A, and also in the occurrence of three nodes between them. Usually in the exceptions the inflorescences arose at a node, and more than three nodes occurred between them.

The above records show that although the characters in question are not constant they are very regular, and that they are correlated to the form of the inflorescence.

F_3. *Fruit Shape.*

Some interesting cases have occurred in regard to fruit shape in the F_3 generation. The longs all bred true to length, but they are not all constant to shape. Family No. $\frac{10}{14}$ (Plate VI, fig. 15) is a case of a full long throwing pyriform longs, the actual numbers being fifteen full longs to three pyriform longs[1].

Family No. $\frac{8}{14}$ (Plate VI, fig. 16) is a pyriform long which has thrown a type with a further constriction at the neck of the fruit. This type I have not previously seen, and owing to its similarity in shape to the calabash gourd, I have named it calabash: it appeared

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[1] Price and Drinkard found that their pyriform types were recessive to unconstricted types, and they state that pyriform types are correlated with a peculiar structure of the corolla. In the case of my pyriform types this was not evident, and no difference is apparent in the flowers of the calabash and pyriform types, but there is an anatomical difference in the various types of fruits.

in recessive numbers, the family consisting of sixteen pyriform and four calabash, a straight 3 : 1 ratio.

One family was constant to full long and one to pyriform long.

Family No. $\frac{1}{1}$ (Plate VII, fig. 19) is a family from a full-long parent, and, as can be seen, there is a slight variation in the shape of the fruit of individual plants. But such differences are not infrequent.

It appears that the full longs have two factors which constitute the shoulder of the fruit, and that in the absence of one factor the fruit is pyriform, and in the absence of both it is the calabash type.

Family No. 12 (Plate VII, fig. 18) throws considerable light on the .genetics of fruit shape; the fruit of the parent was conical and bilocular (as in fruit No. 2 of Fig. 18). A few of the fruits were however round and had three or four cells which, as is previously stated, is characteristic of the F_1 plants. This plant gave four distinct shapes—conical, round, long, and plurilocular compressed fruits.

	AB	Ab	aB	ab
	conical	round	long	compressed round
Observed	29 :	6 :	14 :	3
		35[1]		
Expectation based on a 9 : 3 : 3 : 1 ratio	28·62 :	9·54 :	9·54 :	3·18
		38·16		

The last type appeared in recessive numbers 3 in 51, or approximately 1 in 16. These fruits are large and somewhat corrugated, like those of many cultivated forms. The plurilocular, large, compressed fruits, as in Fig. 18, Nos. 28, 38, 39, is evidently a recessive appearing as 1 in 16; the long members of the family contain B, one of the two factors concerned; the round contain the other, A; and the conicals contain both; but until further experiments are completed, it is not possible to assign the properties of these two factors with perfect confidence.

On the above hypothesis the longs are in excess, but further evidence is required to show if it is of any significance or merely accidental.

The compressed round fruits always have many cells, and the rounds also, but in a less degree. The compressed round form average about seven cells, and the round three or four, but occasionally they have only two. This is characteristic of the original ♂ parent (Lister's Prolific).

It appears that the shape of the fruit and the number of loculi are correlated, and that in the absence of the factor B the fruit is

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[1] It is difficult to grade the rounds from the conical with certainty.

plurilocular, but that when A is present as in the round fruit, there are not so many cells as when both A and B are absent as in the compressed rounds.

At first it appeared that a constant correlation existed between long fruit and the bilocular character, as all the longs which appeared in the F_2 were constant to two cells, and some F_3 families remained quite constant to this character.

Three long fruits however occurred with three cells, but only these three were found to have more than two cells after examining several hundred fruits.

From the results of Family $\frac{12}{14}$, the fruit of the original ♀ parent (Wonder of Italy) apparently possessed the factor B and the original ♂ (Lister's Prolific) A.

Family $\frac{2}{14}$ (Plate VII, fig. 19) is a family analogous to $\frac{12}{14}$, the zygotic results being:

$$AB \text{ and } Ab \; : \; aB \; : \; ab$$
$$\underbrace{\phantom{AB \text{ and } Ab}}_{14} \qquad \quad 4 \qquad 1$$

Family $\frac{3}{14}$ (Plate VII, fig. 19) is apparently a homozygous conical, and is the only true breeding conical that has at present been isolated.

The individual fruit $\frac{5.9}{14}$ (Fig. 17) appears to be a round that has lost a factor at the shoulder of the fruit, in a similar way to the pyriform longs, and probably it is related to the rounds as the pyriform longs are to the full longs. It is the only plant with that shaped fruit that has appeared, its parent being a F_2 conical, and it is curious that more of this type have not appeared[1].

Although the above work on the inheritance of fruit shape is preliminary, the facts show that many mendelian factors are involved, and doubtless further investigation will assist in elucidating them.

All the F_3 families illustrated in this paper are homozygous for the compound type of inflorescence, and it is possible that some forms of fruit, such as the compressed rounds in family $\frac{12}{14}$, may prove to be of economic value, and theoretically they should be homozygous for fruit shape.

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[1] In many families containing conicals, rounds and longs, constricted longs occurred, but no constricted rounds or conicals. Further experiment may nevertheless show that some of the constricted types now classed as longs are really constricted conicals.

STERILITY OF ANTHERS.

The stamens of the tomato are syngenesious, and form a cone round the stigma. Usually the surface of the stigma is slightly below the apex of the cone, and close to the pores in the anthers from which the pollen dehisces. The tomato is therefore well adapted for self-pollination, and when the flowers are in a receptive condition any mechanical movement of the plant further assists in the dispersion of the pollen; the stigmatic surface being also partially protected by the stamens, the chances of cross-pollination occurring are few. Insects of any kind rarely visit the flowers. Those which do are mostly small, and they usually confine themselves to the base of the flower. With close observation I have not on any occasion seen insects near the surface of the stigma.

In 1913 my attention was attracted to two individuals in the F_2 family growing in the open which failed to set fruit. Upon examining their flowers I found the stamens were reflexed and somewhat aborted, and that the stigmas were exposed and protruded about an eighth of an inch beyond them. At first I concluded that it was due to this structural difference that no fruit developed, as I assumed that this would prevent self-pollination. Some time afterwards many of the anthers were examined and found to be contabescent and devoid of pollen. (Plate VI, fig. 14.)

Later these plants produced many parthenocarpic fruits, doubtless without any sexual process. Upon examining a considerable number of these fruits only two were found which contained any seed; one had two, the other only one. These were probably due to cross-pollination; the protruding stigma would be favourable to it occurring should pollen be conveyed by wind from neighbouring plants.

The flowers on an inflorescence of one of these plants were isolated and crossed with the original ♀ parent; the resultant fruits were full of seed and much larger than those without seed. The following year twenty plants were raised from the above cross, and they were all hermaphrodite; the stamens were normal, and they produced fruit freely.

In potatoes Salaman (3) found that the sterility of the anthers behaved as a dominant. He refers also to Darwin's (1) observations on sterility of anthers, which condition when the anthers were aborted he called "contabescence," following Gärtner.

It is of interest to note that the ♀ plant used in this cross was the type with simple inflorescence, and in the F_1. Eighteen plants were simple and two compound. It appears therefore that the ♀ plant was heterozygous.

In *Lycopersicum peruvianum* I have observed that the stigma protrudes considerably beyond the stamens. Many attempts have been made to cross this species with varieties of *esculentum*, but all have failed, in whichever way the cross was attempted.

DESCRIPTION OF PLATES.

PLATE I.

Fig. 1. Inflorescence and fruits of "Wonder of Italy" ♀, "Lister's Prolific" ♂ and F_1 from these.

Fig. 2. Fruits and loculi of parents and F_1 plants. The remainder are some F_2 types.

PLATE II.

Fig. 3. An inflorescence of "Wonder of Italy," showing the large dimensions it acquires.

Fig. 4. Left figure is "Wonder of Italy" and right figure "Lister's Prolific." Illustrates the position of the inflorescences.

PLATE III.

Fig. 5. Left figure is an inflorescence of an F_2 plant, showing the dichotomous branching of the compound forms. Right figure shows an F_2 simple form of inflorescence.

Fig. 6. Inflorescences of two F_2 plants. Right figure is the parent plant of family $1\frac{3}{4}$.

PLATE IV.

Fig. 7. An F_2 plant, showing the characters of the plants with the simple type of inflorescence, namely the occurrence of three nodes between the inflorescences and the internodal position of the inflorescence.

Fig. 8. An F_3 plant, showing the same as Fig. 7.

Fig. 9. An F_3 plant, showing the characters of the plants with the compound type of inflorescence, namely the occurrence of six nodes between the inflorescences and the nodal position of the inflorescence.

PLATE V.

Fig. 10. A plant with the compound type of inflorescence at an early stage, showing the inflorescence at the termination of the main axis.

Fig. 11. A plant with the compound type of inflorescence, showing the fusion of the inflorescence to the lateral growth.

Figs. 12 and 13. Two compound types of inflorescence, showing the regularity of the fruit. It will be noticed that these inflorescences do not bear foliage, as do most of the other compound types which are illustrated.
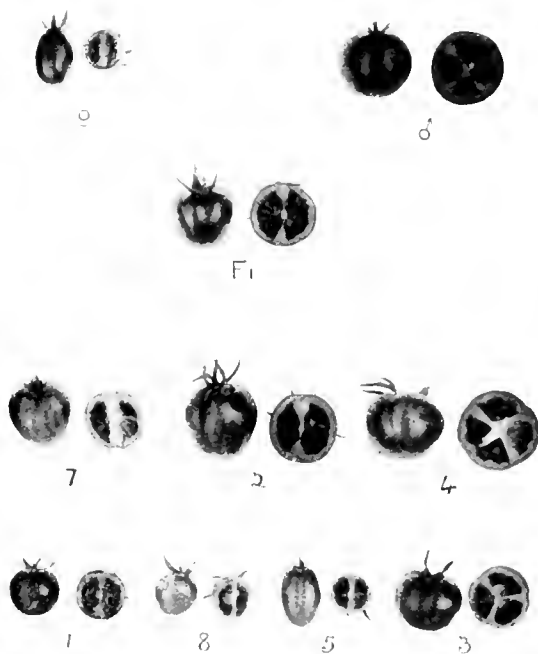
Fig. 1.

Fig. 2.

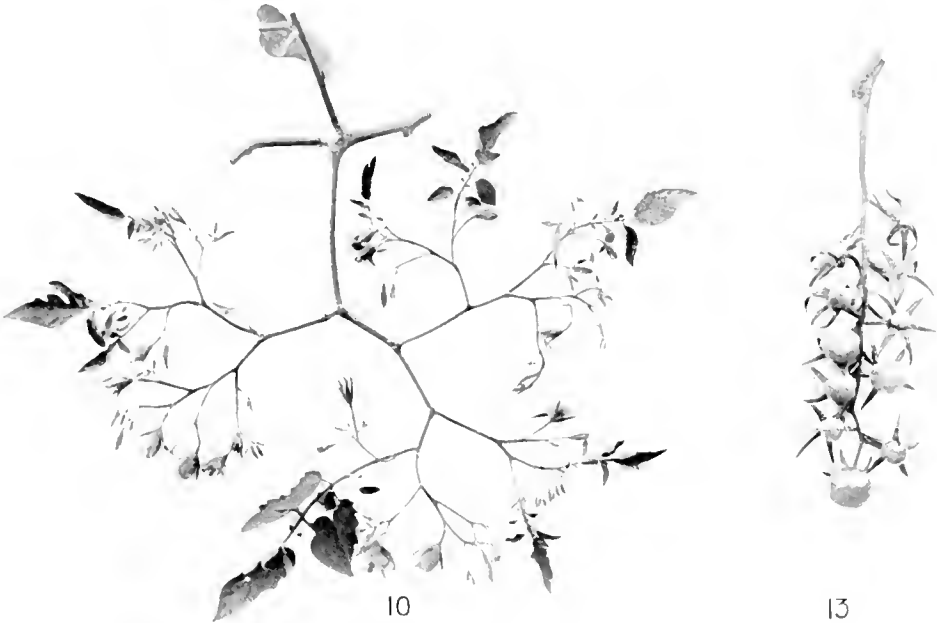Fig. 3.　4 feet across.

Fig. 4.

Fig. 5.

Fig. 6.

PLATE IV

Fig. 9.

Fig. 8.

Fig. 7.

PLATE V

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.
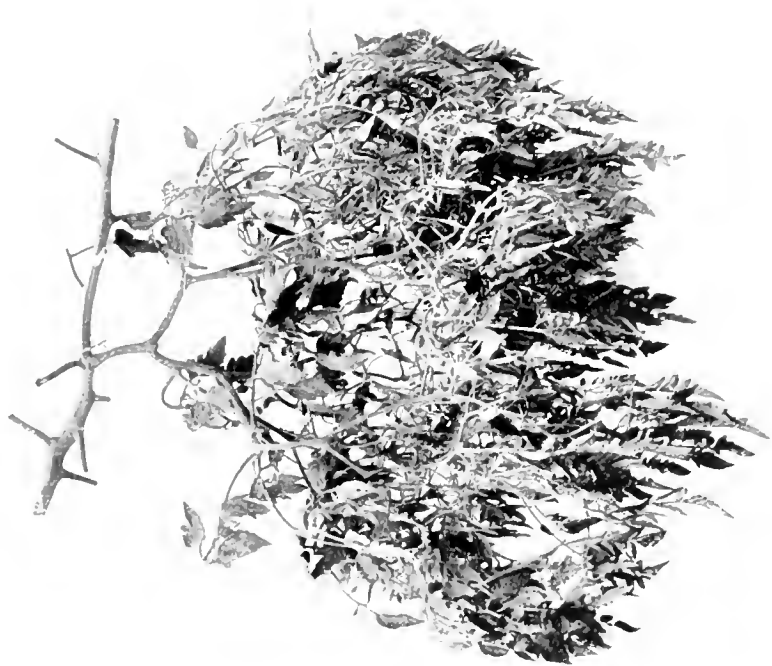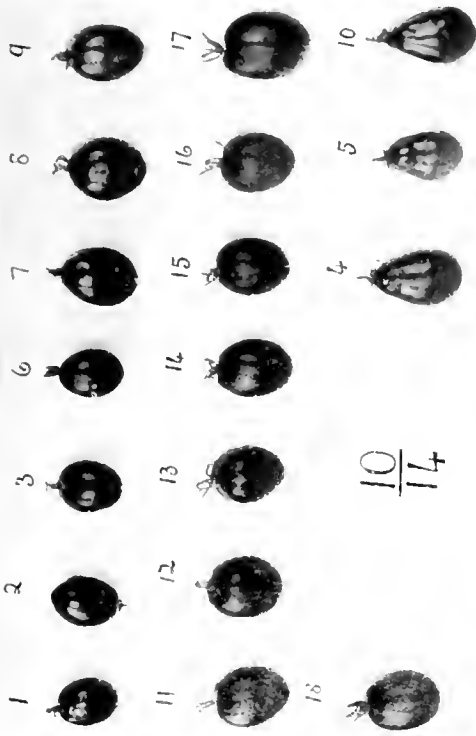
Fig. 15.
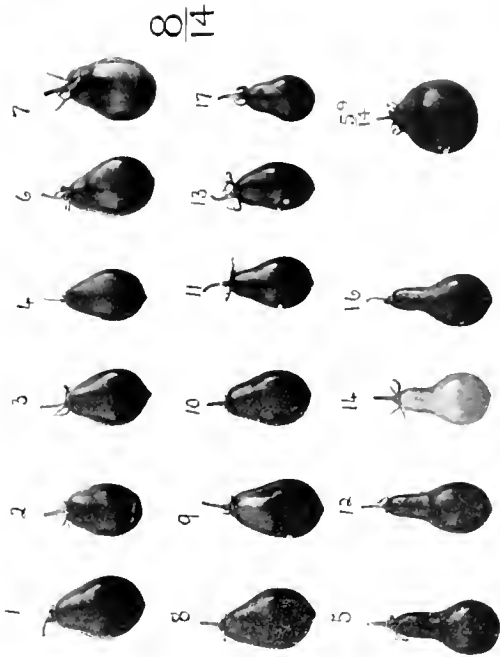
Fig. 16.

Fig. 17.
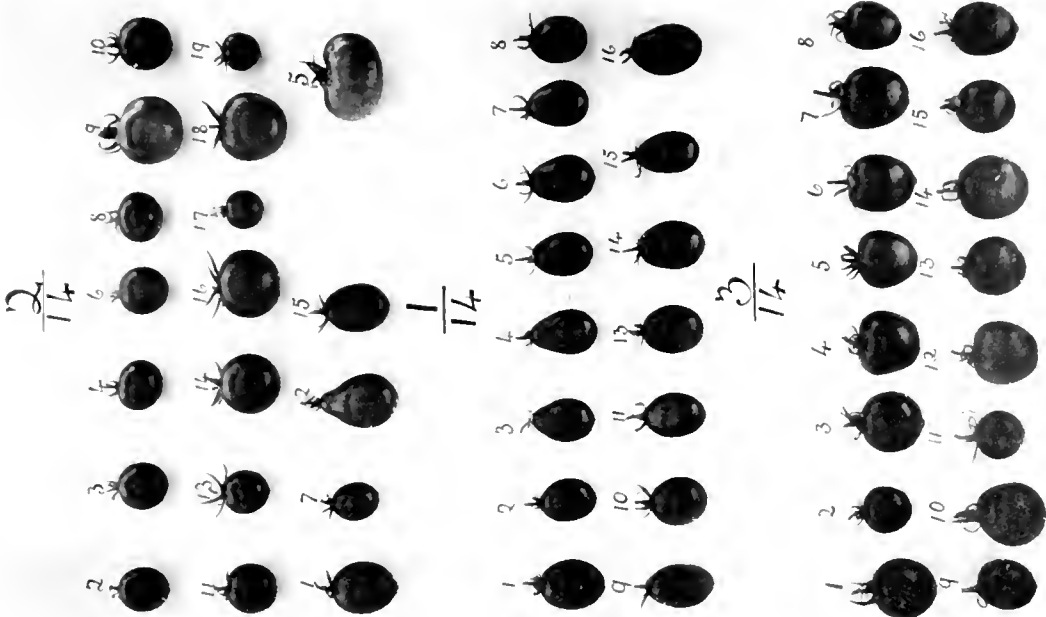
Fig. 14.

PLATE VII

Fig. 19.
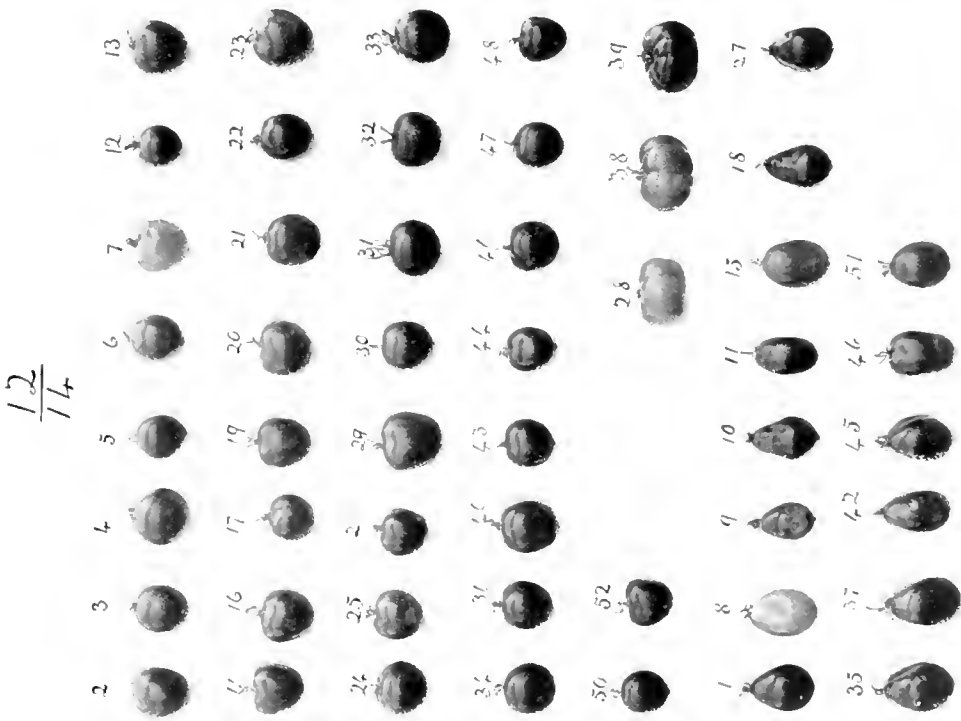
Fig. 18.

PLATE VI.

Fig. 14. Shows an inflorescence of one of the plants which occurred in the F_2 family with contabescent stamens.

Fig. 15. Fruits of family $\frac{19}{1}$. Nos. 4, 5 and 10 are the pyriform longs, the others are full longs.

Fig. 16. Fruits of family $\frac{5}{1}$. Nos. 5, 12, 14 and 16 are the calabash type, the remainder pyriform.

Fig. 17. The individual fruit $\frac{5}{1}$ 9 is the constricted round type.

PLATE VII.

Fig. 18. Showing the fruits of family $\frac{19}{1}$; the rounds are not separated from the conicals. Nos. 4, 17, 24, 31, 32 and 34 are probably genetically rounds. Nos. 28, 38 and 39 are the compressed rounds, and the bottom two rows are the longs.

Fig. 19. Family $\frac{5}{1}$ is similar to $\frac{19}{1}$. No. 5 is the compressed round, and Nos. 1, 7, 12 and 15 are longs.

$\frac{1}{1}$ is a family from a full long parent, and family $\frac{3}{1}$ is apparently homozygous for conical fruit shape.

The numbers of the fruits in the illustrations were the numbers of the individuals in the families from which they came. In all cases the fruit illustrated is a typical representative.

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ON THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (*PISUM SATIVUM*).

By W. BATESON, M.A., F.R.S., *Director*

AND CAROLINE PELLEW,

Minor Student of the John Innes Horticultural Institution.

MANY, perhaps most, varieties of culinary peas (*Pisum sativum*) at present in cultivation are liable to throw "rogues" of a peculiar kind which may be described in general terms as wild and vetch-like. The proportions in which these rogues occur under commercial conditions are of course various, depending on the care with which the parent crop had been rogued, on the nature of the variety, etc. In a crop of Gradus considered fairly free from rogues we estimated the proportion at 1 per cent., but we have seen crops more nearly free from rogues and of course several much worse.

For some years we have been investigating at this Institution the genetic relations of these rogues to the typical varieties from which they come. The main problem remains unsolved and the work is still in progress, but the facts already established are so unusual that it seems desirable to make them generally known. So far as we are aware the case is as yet unique.

The term "rogue" is applied by English seed growers to any plants in a crop which do not come true to the variety sown. For example, tall plants found in a crop sown as dwarf, coloured plants in a white variety, plants with pods of a wrong shape, or in any other way differing from the standard type of the variety are called "rogues." It is the universal practice of all good seedsmen to exterminate these untrue plants every year at some stage before the crop is gathered.

When peas are grown for seed on a commercial scale it will readily be understood that untrue plants are introduced in various ways,

mixture, crossing by insects, and the persistent recurrence of a recessive form being the most obvious sources of such plants. Rogues referable to these several origins we have of course seen among peas, but the facts preclude the supposition that the special rogues with which we are here concerned are introduced either by mixture or crossing, nor can they be regarded as recessives coming from a heterozygote in the ordinary sense.

Preliminary Statement of Results.

By Messrs Sutton's advice we began our work in 1911 with Ne Plus Ultra (N. P. U.), Early Giant (E. G.) and Duke of Albany (D. A.). For some unknown reason N. P. U. did badly on our land, suffering so much from bacterial disease that after 1912 we gave it up. Our observations therefore relate mainly to E. G. and D. A. These two differed considerably in the fact that whereas typical D. A plants with us have thrown no obvious intermediates between type and rogues[1], such plants do occur in E. G. and their behaviour raises some curious problems. Our experience of all three varieties may be summarized as follows :

(a) *Thoroughly typical plants do occasionally throw rogues (E. G. and D. A.) and certain intermediate forms (E. G.).*

(b) *The rogues, of whatever origin, when fertile[2], have offspring exclusively rogues (N. P. U. ; E. G. ; D. A.).*

(c) *Intermediates (raised from types) showing combinations of type and rogue characters give mixed families of various compositions (E. G.).*

(d) *Crosses between types and rogues, however made, have (with the rare exceptions mentioned in E. G.) always given rogues though these in their juvenile condition are generally type-like ; and these rogues have always given only rogues (N. P. U. ; E. G. ; D. A.).*

Description of Rogues.

Foliar Parts.

Most of the best modern forms of culinary peas have the stipules, leaflets, petals, and pods, large and broad. Among these typical plants the rogues are distinguished at once *by the smallness of their*

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[1] See later, p. 29, *note*.

[2] Sterile rogues occur as rare exceptions.

appendicular parts. They are at least as tall as the types, generally perhaps slightly taller, but their stipules, leaflets and petals are comparatively small and narrow, though the plants are perfectly healthy and well grown. The length of the foliar parts is also reduced, but to the eye the greatest difference is in width. Probably in consequence of this diminished extension the stipules of the rogues end in a point formed by the acutely converging edges. The stipules of the types have much more obtuse or even rounded apices, and their bases are full and bulging. The leaflets of the rogues differ similarly from those of the types. In both the midrib ends in a fine, hair-like spine. In the type this stands on an emarginate, truncated end, the curve of the leaf springing about at right angles from the spine. In the rogue the shapes of the leaves vary considerably according to their position on the stem. Those at the upper nodes are scarcely truncated if at all, and the sides of the leaflets converge acutely to the spine. Lower down the stem the leaflets approach more nearly to the typical shape, but are distinguishable by their less ample development. (See Plates VIII and IX, figs. 1—5.)

The types with which we have chiefly worked, Duke of Albany and Early Giant[1], have the foliar parts much marbled on the upper sides with white. This marbling is due to air-spaces under the epidermis. It is often developed to some extent in rogues, but never so much as in types, and in the upper leaves of the rogues it is usually not present at all.

The texture of the leaves also differs, those of the rogues being stiffer and harder, those of the types being more limp and cockled, indicating probably a want of complete correlation between the rates of growth of the several layers.

Pods.

The pods contain as many seeds as those of the types, but those of rogues in E. G. and D. A. with great constancy *curve upwards along the dorsal suture.* In seeking for characters positively distinguishing these rogues the curved pod is one of the most definite and easy to recognize. There are varieties of peas having curved pods as a normal character (e.g. the Serpette peas, Pois d'Auvergne, and Gladstone), and it is possible that the curvature seen in these varieties is genetically of the same nature as that of the rogues; but however that may be, the

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[1] Early Giant is the name by which Messrs Sutton designate a special strain of the well-known Gradus.

curved pod is, so far as we know, always found on these rogues, though on the types from which they are derived all well grown pods have the dorsal edges straight for most of their length[2]. These differences in shape are evidently all expressions of differences in proportional growth along the several axes, and we incline to regard them as various consequences of a deficiency of extension of the foliar parts in the rogue, but we are not able to analyze the phenomena further   (See Plates XII and XIII, figs. 10—15.)

In the rogues of E. G. and D. A. the curved pods are, as we have said, a striking feature.   Attention should however be called to the circumstance that the pods of both these varieties are *pointed*.   In N. P. U. they are *blunt* and the pods of rogues from this variety are straight.   Moreover the Serpette and other varieties normally curved have also pointed pods; and though our evidence on this question is insufficient we are inclined to regard the blunt-ended pod as incompatible with a full degree of curvature.

Seeds.

In shape and colour the seeds of the types and of the rogues are not distinguishable from each other, but those of the rogues are slightly smaller (see later).   There is however a difference in flavour, those of the rogues, whether raw or cooked, being less sweet to the taste than those of the types.   The starch grains of the two forms appear identical. Estimations have been made of the amount of sugar in type and rogue seeds, but so far no consistent difference has been discovered.   Probably therefore the chemical distinction, which must certainly exist, is more profound.

Production of Rogues by the Types.

At first sight it seems improbable that the thin, weed-like rogues can be actually the offspring of the luxuriant types, and we suspected the case to be one of accidental mixture.   Rogues however, apart from their special features, have the characteristics of the types among which they occur.   They flower at the same time whether early or late, their pods are stumpy or pointed according as the type is stumpy or pointed, and so on.   But even if the rogues had arisen originally from the types or simultaneously with them, their perpetuation might be merely due

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[1] In nearly all varieties there is a slight upward curve beginning in the peripheral quarter.

to imperfect sorting[1]. This suggestion however has proved quite erroneous.

We began our experiments by grading the seeds of a commercial sample according to size. We found that the proportion of rogues is actually much smaller among the plants raised from the largest seeds. For example, 302 largest seeds from D. A. and 149 from E. G. gave no rogues; 119 from N. P. U. gave one rogue; but occasional rogues came among the plants both from the medium and the small seed samples. Owing however to fluctuation in size no even approximately accurate sorting can be made in this way.

In D. A. the average weight of well-developed seeds was found to be ·41 g. for the types (9 plants) and ·37 g. for the rogues (5 plants). In E. G. these weights were ·41 for the types (11 plants), and ·34 for the rogues (23 plants)[2]. These differences are considerable, but many type seeds fall much below the rogue average and the seeds of an occasional rogue surpass the type average. In most varieties no doubt by choosing only the very finest seeds the rogues could in general be avoided, but genetic purity cannot be thus attained.

As to the production of the lower forms (i.e. rogues or intermediates) from the finest type plants the details are evidently different for the several varieties; and within the same variety, strains descending from different individuals differ considerably in the liability to throw rogues. The labour of rogueing pea crops is so great that the permanent elimination of rogues would be a matter of considerable economic importance to seed-growers. From our experience however the prospect of attaining that object in the case of the large-leaved varieties at least does not seem very good, though from the great difference between strains a relative purity may perhaps be reached.

The results of sorting the seeds led us to think that it would be possible to raise a pure strain of types. As regards E. G., though of the typical plants raised from the largest seeds some gave families exclusively typical, others threw occasional plants of the lower classes. For example, a type-plant in 1911 gave a family (about 60 plants) in 1912

[1] Certain rogues no doubt are thus perpetuated. For instance, in the case of Veitch's Perfection, a wrinkled pea believed to throw a *round*-seeded rogue, though all round seeds are carefully picked out, experiment showed that the perpetuation of the round-seeded plants was due to the fact that the seeds at the apex of the pods are often so much dimpled as to pass for type seeds, and thus escape the sorters, giving rise of course to round-seeded plants when sown.

[2] The intermediate plants, spoken of later as class 3, gave an intermediate weight, averaging ·37 g. (11 plants).

all types. In 1913 from these were raised 15 families. Some of them contained rogues, but one large family was free from them. From that family in 1914 we raised 29 families, of which 22, aggregating 1122 plants, were all types. The remaining 7 families each contained a single aberrant plant, the total being 357 types and 7 aberrants; or 51 : 1. This is the strain of E. G. which has thrown fewest rogues. Where the proportion of aberrants is so small it is evidently impossible to be confident that plants which give even 100 offspring all typical were incapable of throwing rogues.

In the case of D. A. a much nearer approximation to purity was made. From selected type plants in 1911 about 3300 plants were raised in 1912, all typical. From selected plants among these about 12,000 were raised in 1913, and no aberrant individual was found among them. In dealing with these large numbers of plants it will be understood that the characters of every single plant cannot be positively guaranteed under the conditions of the experiment, for in all such crops there are some plants that have not grown well and might conceivably be aberrant, but we have confidence that no well-grown plant departed from that type, and only the finest plants were used as parents. From eight well-grown families in 1913 (containing, as we have said, no rogues) the seeds were sown in 1914, giving about 39,000 plants, and among them again no rogue was seen.

One family however had the following history. A type plant in 1911 gave a family in 1912, about 60 plants, all types (except two doubtful, which gave only types in 1913). A typical plant in this family gave about 60 in 1913. The best grown of these, all strictly typical, were harvested *en masse*, and their seed was sown in 1914. The crop consisted of about 5100 plants of which six were rogues of an extremely low grade, being moreover *sterile*[1].

Plants of a similarly very low rogue were seen as great rarities in a crop of Gradus growing for seed in Essex. They, also, were apparently sterile. A leaf of one of them is figured on Plate XI, fig. 9, together with a leaf of the type of Gradus, and one of the ordinary rogues in the crop.

The whole course of the evidence is thus quite inconsistent with the supposition that the rogues appear as regular recessives in the ordinary sense, and we are convinced that the commercial growers are perfectly right in asserting that a strain may breed true for a while and then throw rogues. The question arises, can such rogues have been introduced by insect-fertilisation? As a very great rarity accidental

[1] See p. 29.

cross-fertilisation does certainly take place in peas. In the course of many years experience of peas we have met with undoubted cases at least three times. Twice we have seen a pod of yellow, round seeds on a green, wrinkled variety, and these seeds gave ordinary Mendelian results. Once in a sowing of tendrilled, white-flowered plants one heterozygous for purple and for the acacia character appeared, and this gave a normal Mendelian F_2. A few similar cases also have been given us by Messrs Sutton. These occurrences are excessively rare, happening perhaps once among many thousand plants, even when distinct varieties are grown in large numbers near each other. But in the case of the rogues it must be remembered that there is no large body of rogues from which the fertilisation could take place. They are utterly unlike any modern variety. Great efforts are made to exterminate them, and though doubtless an occasional individual gets missed, it cannot possibly be supposed that these survivors can continually pollinate the surrounding types.

Lastly, in the particular case of Duke of Albany just described the rogues were quite peculiar, and in them the general reduction in size of the foliar parts went far beyond anything we had ever met with in our own cultivations. The leaflets were very narrow and almost strap-like, having also an abnormal neuration resembling fig. 9 C. Plate XI. Nor can these rogues be supposed to have been a special F_2 form extracted from a cross with the ordinary rogues, for in the whole crop there were no other rogue-forms at all. Whether the collateral families which up till now have thrown no rogue will continue thus pure is of course uncertain.

The rogues breed true.

To this statement there has been no exception in any of the three varieties (N. P. U.; D. A.; E. G.). The behaviour of the intermediates in E. G. will be described immediately, but the definite rogues whenever they appear, and however bred, are in our experience incapable of throwing any form higher, that is to say, more like the type, than themselves.

Intermediates in Duke of Albany.

Typical plants of D. A., self-fertilised, with us have not thrown definite intermediates comparable with those thrown by E. G. In any row however plants with somewhat smaller parts may occur, and from a commercial sample we have even raised a strain of such plants. But

in crossing type and rogue in D. A. we raised in 1914 a family ($\frac{35}{14}$) containing two plants resembling the E. G. intermediates (besides three actual rogues). The offspring of these will be seen in 1915.

The intermediates in Early Giant.

Between the rogues having all the characters enumerated above and the types there are in E. G. intermediates of several kinds. These are difficult to classify, but speaking generally, we have been able to recognize besides the types and the rogues a third group which have the curved pods of the rogues combined with stipules and leaflets not markedly different from those of the types. In such plants the development of the foliar parts often though not always varies with their position on the stem, the lower being the most developed and nearest the type, the upper being smaller and more rogue-like. These intermediates judged in their younger stages are not distinguishable from types, and but for their curved pods might often pass unnoticed. The point is not capable of exact proof, but we doubt whether the leaves and flowers of these intermediates are ever quite so fully developed as they are in fine typical plants.

The marbling on these plants varies in amount roughly with the extension of the parts, the most rogue-like being the least marbled.

In addition to this comparatively definite class of intermediates, plants are not uncommon, which, though in most respects typical, yet show a degree of curvature in the pods slightly greater than that of the usual type, or even occasionally a pod so much curved as to be mistakable for that of a rogue. Such plants have not been systematically counted, and the evidence showed that they cannot be regarded as genetically distinct from the types.

On the other side of the scale, among the plants which are unmistakable rogues in all other respects there are variations in the size of the parts, and occasionally one of these plants may have stipules and leaves so large as to suggest that it belongs to the intermediate class. In all these individuals however the pods are thoroughly curved.

To resume: in descending series from the type the plants may be classified thus:—

1. *Types.* Leaves and stipules large and not pointed. Surface marbled. Pods straight.

2. *Types:* as above. Pods occasionally curved, or even all slightly curved.

3. *Intermediates.* Leaves and stipules nearly as in type; but usually declining, especially in upper parts of plant, towards the smaller size and shape characteristic of rogues. Pods definitely curved.

4. *Rogues.* Foliar parts (especially at lower nodes) somewhat larger than those of the ordinary rogues. Little marbling. Pods curved.

5. *Rogues.* Foliar parts small and pointed. Little or no marbling. Pods curved.

This classification is to some extent arbitrary. Owing to intergradation, and especially to the fact that the different parts of the same plant are frequently not uniform, it is not possible to refer the individuals to the several classes with perfect certainty. This applies especially to the distinctions between classes 1 and 2, and classes 4 and 5 respectively, and these minor subdivisions have not been systematically recorded.

Genetic Behaviour.

The offspring of classes 4 and 5 are always rogues. As to the interrelation of these two classes it is remarkable that the great majority of the offspring of class 4 belong to class 5. Nor have we ever had a clear example of a plant which could be reckoned as belonging to class 4 coming as the offspring of class 5. On no occasion has a plant of class 4 bred true to that type, or even given more than a small proportion of plants like itself. In other words, the larger-leaved rogues throw a great majority of the ordinary small-leaved rogues, and these always breed true.

As to the genetic behaviour of the other classes the facts are not wholly clear. Difficulty of course arises from the impossibility of referring the individuals to the various classes with perfect consistency, and the genetic composition cannot be quite certainly determined from an inspection of the somatic characters. Many families contain occasional plants of class 2, namely types in general conformation, but having some slight degree of curvature in one or more pods. Plants of this sort have as a rule proved to be, genetically, types.

Classified however according to the offspring which they produce the whole series of plants (other than the rogues, which, as stated above,

give nothing but rogues) can readily be divided into two main groups according as they produce

    A.   Families consisting of a large majority of typical plants with only occasional individuals belonging to the lower grades.

    B.   Families consisting of few typical plants and a majority of the lower grades.

The plants that have thrown families of the A group were :

        Typical plants of class 1.
        All the plants of class 2 except one.
        Three plants of class 3.

The plants that threw families of the B group were :

        None of class 1.
        One plant which had been reckoned as class 2.
        Thirteen plants of class 3.

FAMILIES OF GROUP A.

Of these there were in all 137 of which the records are sufficiently complete, and of them 77 families, aggregating about 3800 plants[1], contain nothing lower than class 2. These we regard as breeding true to type. The remaining 60 families contained the lower or aberrant plants with greater or less frequency.

Of these 60 families 42 were from parents in every way typical and the immediate offspring of types. They gave

        2154 of classes 1 and 2,
          48 of class 3,
          31 of classes 4 and 5,

or 2154 types to 79 aberrants, viz. 27·3 : 1.

4 families were from parents in every way typical but extracted from class 3 parents. They gave

        243 of classes 1 and 2,
          4 of class 3,
          3 of classes 4 and 5.

or 243 types to 7 aberrants, viz. 34·7 : 1.

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[1] In some families recorded as true before the general course of the phenomena was known we have only estimates of the totals, and hence the precise numbers cannot be given.

11 families were from parents reckoned as class 2. They gave

> 634 of classes 1 and 2,
> 17 of class 3,
> 13 of classes 4 and 5,

or 634 types to 30 aberrants, viz. 21·1 : 1.

The remaining 3 families contained a distinctly higher proportion of aberrants, though these were still a small minority. They gave

> 162 of classes 1 and 2,
> 16 of class 3,
> 9 of classes 4 and 5,

or 162 types to 25 aberrants, viz. 6·5 : 1.

It is likely that these three form a distinct genetic group, and the parents of all three were classified *as belonging to class* 3, which combine the foliar structures of the types with the curved pods of the rogues.

The details of these three families were as follows:

Reg. Number	Classes 1 and 2	Class 3	Classes 4 and 5	Ratio
1914				
122	33	0	4	8·25 : 1
137	50	6	1	7·1 : 1
145	79	10	1	5·6 : 1

The details of the other families cannot as yet be regarded as important, nor can any significance be attached to the particular composition of the first 57 families at all events. Since the frequency of the aberrant plants is so small it is evident that many of the families included among the 77 which contained no aberrants may have been capable of producing them. All that can be positively declared is that individuals, thoroughly typical, are capable of throwing the lower forms sporadically in small numbers, and that the genetic behaviour of classes 1 and 2 is approximately the same.

Families of Group B.

There are 16 families of this kind, namely containing a minority of types and a large majority of aberrants. The proportions seem altogether irregular, and they range from 1 type : 64 aberrants (No. 118) to 1 type : 2 aberrants (No. 112). Of the 16 parents 15 were of class 3 and 1 was of class 2.

The details are as follows :

Parent	Reg. Number	Offspring		
		Classes 1 and 2	Class 3	Classes 4 and 5
	1913			
Class 3	92	6	8	64
,,	113 [1]	0	4	81
,,	117	5	7	89
,,	118	1	2	62
	1914			
,,	116	6	4	28
,,	117	15	8	63
,,	127	7	11	19
,,	128	3	3	81
,,	147	4	61	57
,,	148	2	0	37
,,	160	6	32	21
,,	161	2	10	10
,,	162	2	8	23
,,	173	2	0	21
,,	112	45	8	85
Class 2	155	10	15	13

These 16 families give a total of 116 typical and 935 aberrant, but it is obvious that there is no uniformity in their composition. The last two differ considerably from the rest in containing a distinctly higher proportion of typical plants. The parent of one of these was moreover classed as class 2.

The genetic behaviour of the types and intermediates may now be summarized as follows :

Perfectly typical plants often breed true, but they may throw any of the aberrant forms, though never more than a small percentage of them.

Plants of class 2 commonly behave genetically like the types themselves. We have included in class 2 such plants as have straight pods together with others showing some curvature, but most of this class consists of plants with a low degree of curvature in many pods (as Plate XIII, fig. 15). Those which had any straight pods at all behaved genetically like types. One plant (155) however which had only a slight degree of curvature was proved by its offspring to be of the genetic composition of class 3. Three plants genetically of Group A, were shown by their offspring to differ in composition from most of that Group,

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[1] Though this plant gave no offspring typical it may be included here, because the family is obviously of the same general composition as the rest, and because the families 160–2 descend from it.

inasmuch as they threw a higher proportion of aberrants, and it is noticeable that these three plants (122, 137, 145) had on their somatic structure been reckoned as class 3.

Most of class 3, the real intermediates, must be genetically quite different from the types of classes 1 or 2, for instead of throwing a large majority of types, they give a large majority of rogues.

From what has been said it will be observed that plants with curved pods can throw some plants with straight pods, but plants with rogue foliage cannot throw offspring with typical foliage.

As regards the correctness of our discriminations of the classes when tested by genetic results, it will be observed that in addition to the plant referred to class 2 which behaved like class 3, there were also the three plants assigned to class 3 which behaved like low members of Group A. Judgments therefore based on somatic appearances give in this case a rough, but by no means accurate, indication of genetic behaviour.

Allowing however for some error in the classification of the families, the proportions in which the aberrant forms are produced by the types are such as to make it extremely unlikely that they are expressions of any ordinary factorial system. It might for example be supposed that the type leaves or the straight pods were each dependent on the presence of one or more factors. Any scheme based on the hypothesis that these factors are distributed in any of the ordinary ways must however fail, not merely on account of the rarity of the aberrant individuals of the various classes collectively, but on account of the numerical relations of the aberrant classes to each other. On the other hand an equally unconformable phenomenon appears in the circumstance that the plants of class 3 are able to produce thoroughly typical offspring which breed as true as the types. We have then to reckon with the paradox that the types, without crossing, can occasionally produce the intermediates, and that these, in their turn, can, also by self-pollination, produce types.

From the fact that the rogues never threw any of the higher classes we at first were inclined to regard them as recessives and class 3 plants as heterozygotes, leaving the question of the number of factors involved in abeyance. Since class 3 never breeds true and throws both types and rogues, each of which behaves genetically like the other members of those classes, the suggestion that class 3 is heterozygous seems at first sight plausible; but here again the numerical composition of these families makes any such supposition quite inapplicable

The interrelations of classes 4 and 5 are equally obscure. Inasmuch as class 4 never breeds true, it cannot be regarded as homozygous in the usual sense; nor in view of the fact that it throws almost exclusively plants of class 5, can it be represented in any simple way as heterozygous.

CROSSES BETWEEN TYPES AND ROGUES.

We have next to consider the remarkable evidence provided by the crosses. It relates in the first place to 52 families raised by crossing thoroughly typical plants with rogues of classes 4 or 5. Of these cross-bred families 50, containing 284 plants, *when fully grown*, were

CROSSES.

1. *Type ♀ × Rogue ♂.*

Reg. Number	Female	Male	Number	Offspring	
				Juvenile condition	Adult condition
1912					
88	D. A. type	D. A. rogue	9	—	rogues
89	,,	,,	9	—	,,
90	E. G. type	E. G. rogue	2	—	,,
91	,,	,,	9	—	,,
94	N. P. U. type	N. P. U. rogue	7	—	,,
95	,,	,,	4	—	,,
1913					
337	,,	rogue in "Exhibition"	5	—	,,
338	,,	,,	2	—	,,
1914					
2	E. G. type	E. G. rogue	6	—	,,
3	,,	,,	6	2 ? type	,,
4	,, (class 2)	,,	7	1 ? type	,,
5	,, type	,,	7	5 v. near type	,,
6	,,	,,	6	near type	,,
7	,,	,,	9	,,	,,
8	,,	,,	9	,,	,,
9	,,	,,	1	rogue	,,
10	,,	,,	1	,,	,,
12	,,	,,	4	3 ? type	,,
29	,,	,,	9	near type	,, (2 class 4)
30	,,	,,	1	,,	,,
31	,,	Dwarf rogue	8	7 near type	,,
33	,,	D. A. rogue	8	near type	,,
34	D. A. type	E. G. rogue	8	,,	,, (1 class 4)
57	E. G. type	,,	7	,,	,,
63	,,	,, (class 4)	10	,,	,,
64	,,	,, ,,	7	,,	,,
67	,,	,, ,,	9	,,	,,

thorough rogues in all respects none reaching a development higher
than that of class 4, most of them being class 5. As shown in the
Table these crosses were made not only in Early Giant and in Duke of
Albany but also in Ne Plus Ultra. We have in addition 4 families
raised by crossing E. G. with a rogue from a dwarf variety and 2 from
N. P. U. fertilized from a rogue in "Exhibition."

2. *Rogue ♀ × Type ♂.*

Reg. Number	Female	Male	Offspring		
			Number	Juvenile condition	Adult condition
1912					
92	E. G. rogue	E. G type	2	—	Rogues (some steriles in F_2
93	,,	,,	1	—	see text)
1914					
13	,,	,,	6	1 near type	rogues
14	,,	,,	5	3 near type	,,
15	,,	,,	4	type	,,
16	,,	,,	3	,,	,,
17	,,	,,	4	near type	,,
18	,,	,,	2	,,	,, (1 class 4)
20	,,	,,	5	type	,,
21	,,	,,	7	near type	,, (1 class 4)
22	,,	Dwarf type	9	type	,, (class 4)
23	,,	,,	4	,,	,, (1 class 4)
24	,,	,,	1	near type	,, ,,
25	,,	E. G. type	6	5 near type	,,
32	Dwarf rogue	,,	1	near type	,,
37	D. A. rogue	D. A. type	9	,,	,,
38	,,	,,	5	,,	3 rogues, 2 intermed.
39	,,	E. G. type	6	5 near type	rogues
40	,,	,,	5	type	,, (1 class 4)
43	,,	D. A. type	3	,,	,, ,,
44	,,	,,	8	rogues	,,
45	,,	,,	7	near type	,, (1 class 4)
53	,,	,,	9	,,	,,
70	E. G. rogue (class 4)	E. G. type	3	1 near type	,,
71	,,	,,	5	near type	,,

Crosses between Type and Intermediate (Class 3).

Reg. Number	Female	Male	Offspring		
			Number	Juvenile condition	Adult condition
1914					
49	D. A. type	E. G. class 3	1	near type	rogue*
50	,,	,,	8	,,	5 intermed., 3 rogues
69	E. G. class 3	E. G. type	7	,,	4 type, 3 intermed.
68	,,	E. G. rogue	6	rogues	rogues

* See final note.

Crosses between Rogues and Rogues.

Reg. Number	Female	Male	Offspring		
			Number	Juvenile condition	Adult condition
1914					
51	D. A. rogue	D. A. rogue	9	rogues	rogues
54	,,	E. G. rogue	3	,,	,,
55	,,	,,	6	,,	,,
56	,,	D. A. rogue	8	,,	,,
59	E. G. rogue	E. G. rogue	7	,,	,,
60	E. G. rogue, class 4	,,	7	,,	,,
61	E. G. rogue	,,	7	,,	,,
62	,,	,,	8	,,	,,
65	,,	E. G. rogue, class 4	4	,,	,,
66	,,	, ,,	5	,,	,,

In some the type was used as mother and in others as father, but the results were the same.

Fourteen of these plants which we may call F_1 were bred from and gave 949 plants all rogues, none of which reached a development higher than that of class 5. The F_3 plants were also rogues without exception. This evidence taken together with the fact that no rogue, however produced, has given anything but rogues, may be taken as proving conclusively that the elements, whatever they may be, which cause the distinction between the type and the rogue, are absent altogether from the rogue. The types can produce both intermediates and rogues; the intermediates produce a few types and many rogues, and the rogues breed true[1].

We have stated that the so-called F_1 plants, when adult, were thorough rogues. *In the juvenile condition* however the majority of them, judged by the size and shape of leaves and stipules, differed little if at all from the types. Actual rogues of classes 4 and 5 can be distinguished from types as soon as any leaves appear. By the time the sixth or seventh leaf is unfolded the difference is clear even to the inexperienced. In the case of most rogues bred in F_1 the lower leaves and stipules in size, shape, and marbling are almost if not quite like those of the types, and until about the 8th node is reached we cannot as a rule distinguish them. After that level the narrowing of the parts begins, and the rogue characteristics are rapidly assumed (cp. Plate X,

[1] As it was conceivable that this behaviour of the rogues was due to apogamy, experiments were made to determine whether this phenomenon occurs. No indication of a positive result was however obtained, nor have we ever seen seed formed in the course of many similar trials made in the past with various forms of *Pisum*.

figs. 6 and 7). In some of the families the course of development was not noted, but of 44 families which were more carefully watched most of the members of 34 families are recorded as beginning like types and three families only (10 plants) as beginning in the rogue-like condition.

It might be supposed that the more luxuriant growth of the F_1 seedlings was, as it so often is, an incidental result of crossing; but this suggestion is negatived by the experience of 10 crosses made *between rogues*, giving 64 plants which were characteristic rogues from the first, without any symptoms of extra luxuriance.

Besides the 50 families raised from rogue × type or reciprocal, which behaved in the way described, there were two exceptional cases[1].

1st Exception. In this ($\frac{22}{12}$) an E. G. rogue fertilized by a true type gave 2 seeds of which one grew to be adult. This F_1 plant was recorded as having *leaves like type*, but curved pods. Judging from the offspring it produced, this plant was probably of the kind which we came subsequently to recognize as class 2 namely type-plants with some degree of pod-curvature, behaving genetically as types. In F_2 it gave a family of 38 plants. They were not very well grown, but their characters were in all respects those of *types*, several having pods slightly curved, but none in any way approaching rogues. Two of these gave moreover offspring in F_3, 21 and 57 plants respectively, all well grown plants in all respects typical, occasional pods being slightly curved, as may happen in any family of types.

There is in this case complete certainty that the original *mother* was a rogue, for the normal offspring of that plant have been grown for three generations. All are thorough rogues, and the strain has been used repeatedly for crossing, giving the results which we have come to look on as normal.

Seed of the original father was unfortunately not kept.

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[1] In $\frac{22}{12}$ F_1 from E.G. rogue × E.G. type was a rogue as usual, but among 19 F_2 plants derived from it were 4 steriles. The flowers did not open properly and the pollen was deficient in amount. One artificial pollination failed. Probably this sterility was a recessive condition, but whether it affected one sex or both was not clearly made out. The seed of the parents used in the original cross was not preserved and it cannot be said if sterility existed as a recessive on either side of the parentage. Recessive sterility is of course not uncommon among plants, especially in connexion with the male side. As already stated, we had on one occasion sterile rogues in D.A. It is interesting to notice also that from Andrew Knight's description of his experiments in crossing peas he clearly had a strain affected with male sterility, which phenomenon, in accordance with the scientific ideas of those days, he attributes to prolonged cultivation in one locality (*Phil. Trans.* 1799, p. 196).

2nd Exception. In this ($\frac{35}{14}$) a cross of D. A. rogue × D. A. type gave 5 plants, of which 3 were rogues *and 2 were intermediate*, being the only D. A. plants we have bred which look comparable with the definite intermediates so often bred in E. G. Their offspring will be seen in 1915.

We have no interpretation of these remarkable exceptions as yet to offer.

Crosses with Intermediates.

Since crosses between rogues and types give rogues only (with the two exceptions named), it was to be expected that crosses between rogues and intermediates would do the same. This cross was made only once and gave six rogues ($\frac{68}{14}$).

More interest attaches to the crosses between the intermediates (class 3) and the type. The result of this mating is known in three cases only (see Table, 49, 50, 69). It will be observed that in one case the type E. G. was the father, and in the other two the type D. A. was used as mother. The evidence is meagre, but it supplies proof of the important fact that neither sex of the class 3 intermediates can be homogeneous.

DISCUSSION.

The general course of the phenomena is evidently quite unlike anything with which we are familiar in ordinary Mendelian inheritance. Since the types can throw rogues and the rogues cannot throw types, it seems clear that the types contain something which the rogues do not contain. This something however is different from an ordinary Mendelian factor both in the effects of its presence and in the manner of its distribution among the gametes.

As stated in the introduction the visible differences (apart, that is, from the difference in flavour of the seeds) between type and rogue are essentially quantitative. The distinctions affect the shapes of the organs, but possibly all of them, even the striking difference between straight and curved pods, may be consequences of greater or less extension, and we incline to think that the rogue is really a form wanting in some particular kind of luxuriance or power of amplification. The difference is of course not merely one of size, for rogues may be large and types may be small; but it must be rather some quality of extension, dependent on cell-division occurring chiefly at right angles to the axis of growth.

Since the curved pods may be combined with foliar parts approximately like those of the types, it seemed at first sight possible that these two characters might be governed by separate factors of the familiar kind, but the genetic evidence at once disproves this suggestion. The composition of the families in which rogues appear from types makes any scheme of this kind inapplicable, and the fact that the families derived from intermediates consist chiefly of rogues is of course quite at variance with such a possibility.

As regards the appearance of rogues from types we plainly have to deal with an irregular phenomenon. The gametes capable of producing rogues are given off sporadically and not in accordance with any system that we can perceive. This is abundantly proved by much evidence and especially by the case of the strain of Duke of Albany quoted at the beginning of this paper, in which a strain after breeding true on a large scale for two generations gave rise to six thorough rogues. In view of this irregularity it may be supposed that some phenomenon of mosaicism may be involved. We have much inclined to this hypothesis. Can the type plants or some of them contain "islands" of rogue tissue? When characters are distributed in a plant mosaically, that is, to speak strictly, *not according to any geometrical system*, families of irregular composition are to be expected. The formation of *rogue-gametes* by the types must be describable in these terms, but we can get no evidence that the somatic tissue of the types is thus actually mosaic. We have often sowed seeds from the most curved pods on plants otherwise type, but rogues did not come with increased frequency from such pods. In one case a whole branch had curved pods while another branch was typical, but all the offspring were typical. The evidence suggests that there is a gradation in genetic proportion from the types which breed approximately true to the intermediates which throw a large majority of rogues, the group of three plants which gave only 6·5 types to one rogue forming a connecting link between them. Moreover the fact that these three plants were reckoned as of the intermediate class when judged by their somatic characters, proves that the somatic gradation imperfectly corresponds with the genetic. But there is still a wide gap between 5·6 types to one rogue as found in family 145 (p. 23) and one type to two rogues as found in family 112 (p. 24).

No hypothesis of mosaicism, even if otherwise probable, will represent the results of crossing types with rogues, which are, so far as we know, without any close parallel among plants or animals. We must suppose that the gametes concerned in the production of the cross-bred

plants *are those which would take part in self-fertilisation,* and that we are not concerned with any phenomenon of selective fertilisation. The results of the crosses must therefore be in reality heterozygous and must receive from the one type-parent those elements which if they were united with a similarly constituted gamete of the other sex would form a type-plant. Nevertheless such plants are rogues and breed rogues only. Therefore the type-elements received by the F_1 from the type-parent must be permanently lost. Whither do they disappear? *The only answer to this question which we can offer is that when introduced from one side only of the parentage these elements are in some way used up and cut out of the germ-lineage in the early stages of the somatic development.* The young stages of the F_1 plants are, almost always, type-like, but the characters of the type are left behind with further development.

We have also evidence that a similar change takes place in the life-history of some at least (probably most) of the rogues which come as the immediate offspring of types. Several times families afterwards found to contain rogues, though individually examined in the early stages, were then recorded as free from rogues; and occasionally in these families plants which developed into ordinary rogues are recorded in the juvenile condition as doubtful. Rogues, offspring of rogues, never pass through such a stage. There is therefore no reasonable doubt that the rogues arising as the offspring of types are at all events frequently heterozygotes formed by the union of type and rogue gametes, and since they always breed true, in them also the type-elements must be lost in some somatic stage.

Some light may perhaps be obtained by examining the produce of seeds from the various parts of the plant separately and this we shall endeavour to do, but it is likely that by the flowering stage the differentiation, or segregation if the term be applicable, has already been effected. Nevertheless in plants of the intermediate class the apical parts are so much more rogue-like than the rest that the experiment ought to be made.

We incline to think these indications point to some process of somatic segregation which prevents the type-elements from reaching the germ-cells of the cross-bred plant. A comparison may perhaps be suggested between this phenomenon and the examples, fairly frequent in horticultural literature, of plants which produce from root-cuttings forms different from those arising by the propagation of shoots or buds above the root-system.

It may be mentioned that the genetic behaviour of the ordinary factors introduced in crosses with rogues is normal. For example the rogue F_1 from D. A. × E. G. bears the usual yellow and green seeds. One of our D. A. strains throws albino seedlings which die. Such albinos appear as normal recessives among the offspring of F_1 rogues raised from crosses with that strain, and other similar instances have occurred. Clearly therefore there is no general exclusion of the contribution of the type-parent, and it is only the features special to the type which are excluded.

The nature of the difference between Type and Rogue.

The genetic behaviour is, as we have said, without parallel, and even for the differences themselves there is no very plain analogy. The most obvious is that distinguishing giant forms from those of ordinary size in several plants, especially in *Primula*. Provisional counts of the chromosomes in the peas have not shown numerical differences, but our experience of such work is small and pending an expert report which we are obtaining, the matter must be regarded as doubtful. In *Primula sinensis* however Gregory has described a giant race differing greatly in size from the ordinary type though the chromosomes were not more numerous. But in no case, so far as we know, in which giant forms have been observed, do these throw offspring in any way comparable with our rogues. Nothing of the kind is recorded for *Primula kewensis*, *Oenothera gigas*, or either of the giant forms of *Primula sinensis*. In genetic behaviour all these cases differ entirely from ours.

In this connexion perhaps the case of tulip "thieves" may be mentioned. These plants arise from ordinary, broad-petalled tulips, and are distinguished by their narrow, pointed petals[1]. As to their genetic properties we have no information, but the differences between them and the type from which they come is somewhat suggestive of those with which we have dealt.

Messrs Sutton have called our attention to somewhat similar rogues with *erect* pods thrown by Broad Beans (*Vicia faba*) with drooping pods. We have begun to investigate this case, but we incline to suspect that these rogues are in reality derived from crosses with the variety known as the Horse Bean, in which the pods are erect.

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[1] Solms-Laubach, *Weizen und Tulpe*, Leipzig, 1899, p. 71 ; and Krelage, *Gard. Chron.*, 1881, ii. p. 182.

Historical Evidence.

Messrs Sutton have most kindly made a search of their trial-records back to 1886 in the hope of discovering something as to the frequency of rogues in the history of well-known varieties. There are continuous records of the following:

American Wonder, Blue Peter, British Queen, Champion of England, Daniel O'Rourke, Dr McLean, Duke of Albany, Earliest Blue, Eclipse, Fillbasket, McLean's Little Gem, Ne Plus Ultra, Pride of the Market, Prince of Wales, Sangster's, Telegraph, Telephone, Triumph, Veitch's Perfection, Walker's Perpetual, Yorkshire Gem, Yorkshire Hero. The trial sample in each case consists of 200—300 seeds. Of the varieties named, the following six have produced rogues with especial frequency: Dr McLean, Duke of Albany, Ne Plus Ultra, Pride of the Market, Telegraph, Telephone. Plants not true to type of course may come occasionally in any variety, but the "wild" rogues with which we are concerned are only rarely recorded as appearing in the other 16 varieties. It is perhaps worth noting that all the six are varieties characterized by the great width of the leaves and stipules. On the other hand Fillbasket, of which Denaiffe remarks "feuillage...particulièrement léger pour une race demi naine," is not once recorded to have thrown one of these rogues.

Certain varieties have pods curved as a normal feature, and, since they have already one of the definite rogue features, it might be expected that they would commonly throw rogues. It is noticeable however that, according to several trials recorded by Messrs Sutton, the variety Gladstone threw no rogues in our sense, though this variety has pods markedly curved. Of other curved types we have no evidence.

From the indications given we incline to think that the production of rogues is a consequence of some instability connected with great lateral extension of the parts.

From the genetic evidence[1] it is clear that in order to influence the somatic structure beyond the juvenile stage, or to appear in the germ-cells, the character, whatever it is, must be introduced from both sides of the parentage.

In the business of harvesting we have had the benefit of much assistance from many workers at this Institution, to whom our thanks are due. During 1914 also, Miss Ida Sutton, one of our Minor Students, took part in recording and generally in the experimental work.

[1] The exceptions must be remembered.

[*Note added June 1915.* The paper gives results to end of 1914. The work of 1915 has added one point of considerable importance. The cross-bred plant 49 of 1914 (p. 27), booked as rogue, had a branch somewhat type-like in character, the next being thoroughly rogue. Seed saved from the rogue parts have given all rogues, but the seed of the type-like branch has given some type-like plants in addition to many rogues. Details will be given in a later communication. The case is of considerable significance as adding not only another exception to the general behaviour of the crosses, but also actual proof that a plant can be a true mosaic of rogue and type.]

EXPLANATION OF PLATES.

PLATE VIII.

Fig. 1.   Stipules and leaf of type (Early Giant).

Fig. 2.   Another leaf of Early Giant.

Fig. 3.   Comparable stipules and leaf of Early Giant rogue.

These three figures are from plants grown in pots indoors. They were drawn by Mr Osterstock.

PLATE IX.

Fig. 4.   Stipules and leaf (right hand) at tenth node of Duke of Albany.
      ,,   ,,   (left hand) at top of stem.

Fig. 5.   Stipules and leaf of Duke of Albany rogue. Left-hand figure from fourteenth node. Right-hand figure from top of stem.

PLATE X.

Fig. 6.   *A.* Stipule and leaf from sixth node of a young seedling Early Giant type. *B.* The same from the seventh node of the same plant, showing shape of the apex of leaf when folded. *C.* The same parts from a seedling Early Giant rogue. *D.* The same from the seventh node of the same plant, showing shape of the apex of the leaf when folded.

Note that in *B*, the type, the apex of the leaf is cut square, whereas in *D*, the rogue, it is pointed.

Fig. 7.   Stipules and leaflets of F_1 seedlings (type × rogue). *A.* Stipule of sixth node. *B.* Leaflet of sixth node. *C.* Leaflet of seventh node before unfolding. *D* and *E.* Stipule and leaflet of fifth node. Note resemblance of these parts to those of type plants.

PLATE XI.

Fig. 8. Rogue resulting from the cross type × rogue in Early Giant.

    A. Stipule and leaf of ninth node.

    B. Stipule and leaf of twentieth node.

Fig. 9. *A*. Leaf of Early Giant type.

    B. Leaf of Early Giant rogue.

    C. Leaf of sterile rogue found in Gradus (p. 18).

All these three are taken from above the middle of the stem.

PLATE XII.

Fig. 10. Whole plant of Early Giant rogue, Class 5.

Fig. 11. Whole plant of Early Giant rogue, Class 4.

Fig. 12. Whole plant, Intermediate, Class 3, with foliage much as in the type, even to the top of the stem, but *pods curved* as in rogue.

Fig. 13. Early Giant type. At top of lateral stem is one curved pod (see p. 20).

PLATE XIII.

Fig. 14. Pods. *A*. Straight as in Early Giant type.

    B. Curved, as in Intermediate, Class 3.

    C. Curved and narrow, as in rogue.

Fig. 15. All the pods of a plant of Early Giant which bore both straight and curved pods. Chosen as an extreme case of approach to Class 3; but like other such plants bearing this mixture of pods it was proved by its offspring (20 typical) to be genetically a type of Class 2.

Fig. 2.

Fig. 1.   Fig. 3.

PLATE IX
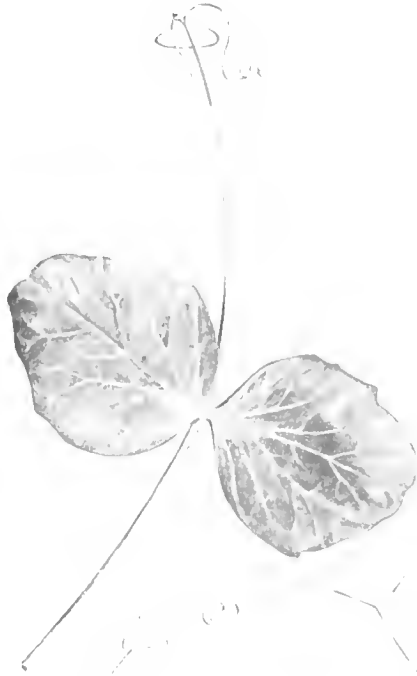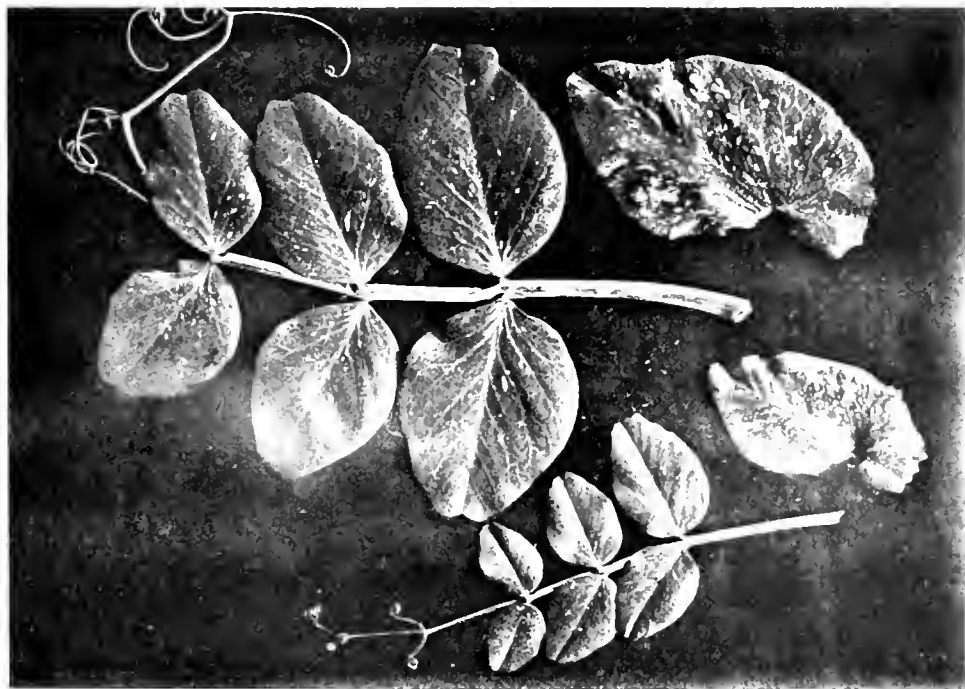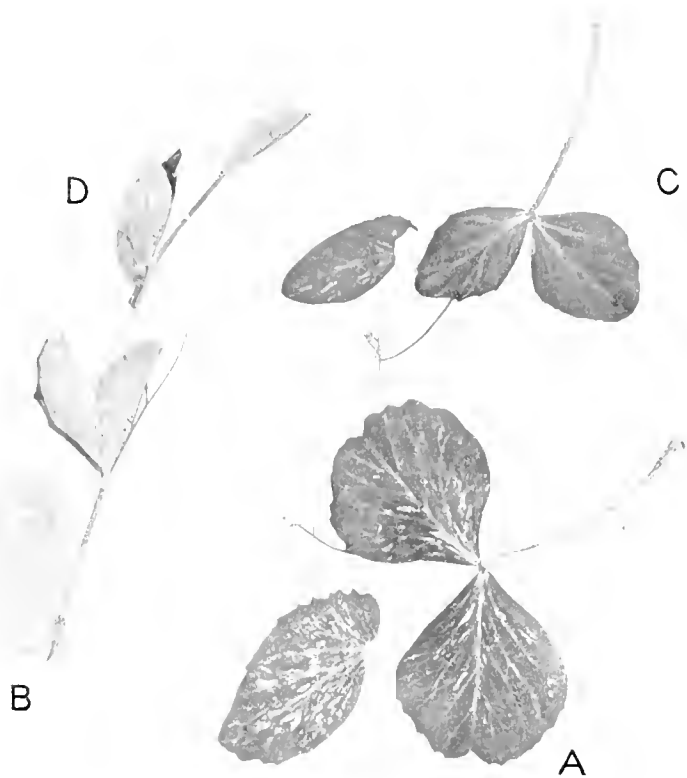
Fig. 6.
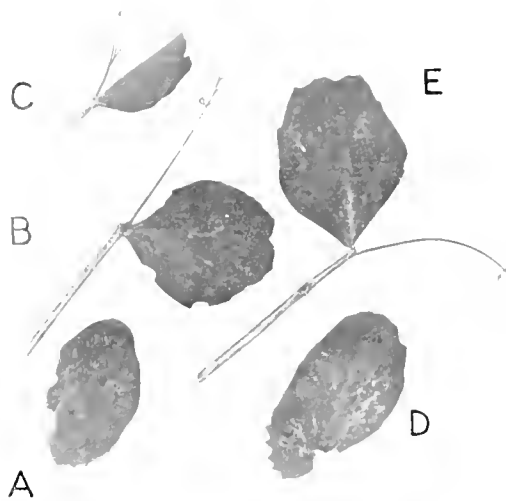
Fig. 7.

Fig. 8.
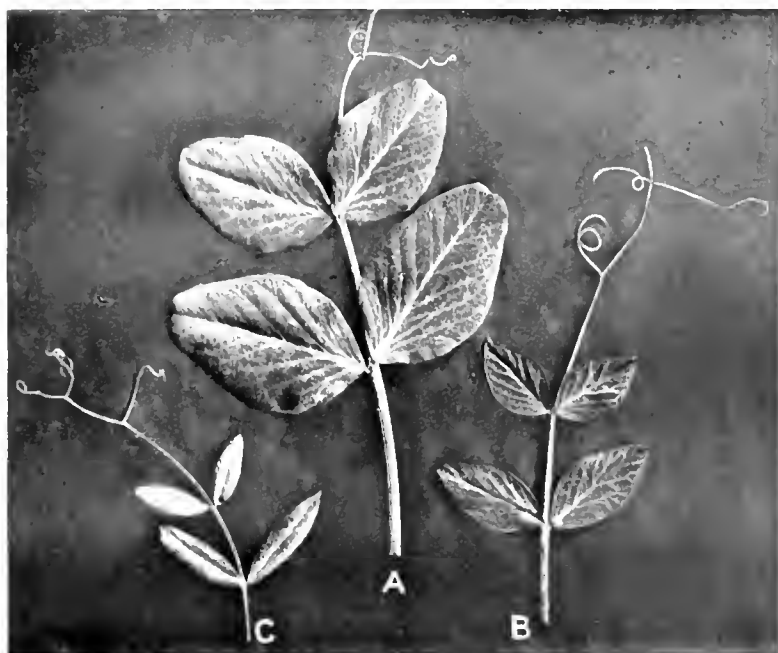
Fig. 9.

Fig. 13.
Early Giant Type.

Fig. 12.
Class 5. Type foliage. Rogue pods.

Fig. 11.
Rogue, class 4

Fig. 10.
Rogue, class 5.
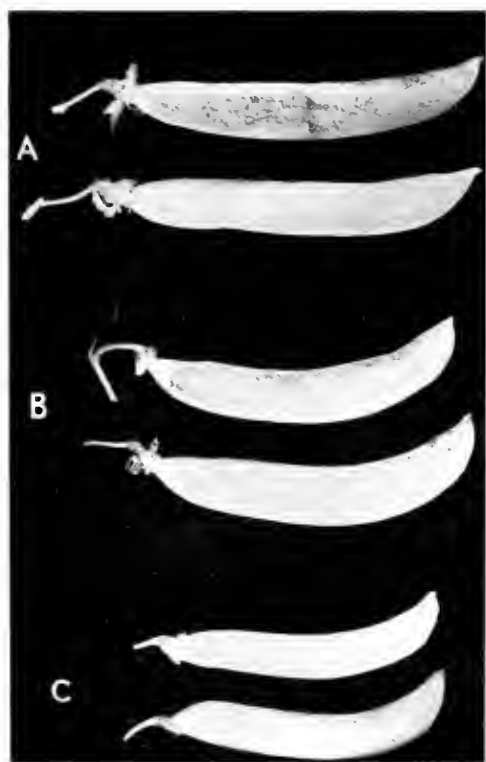
Fig. 14.
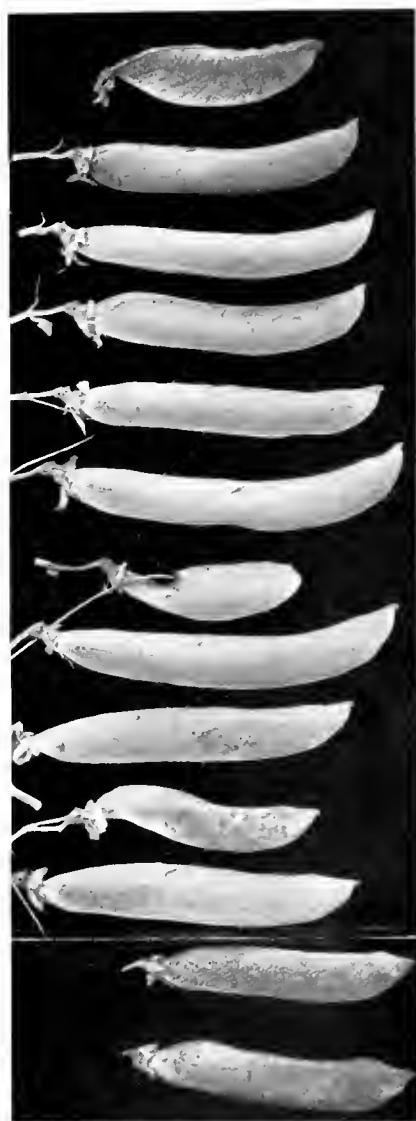
Fig. 15.

FURTHER EXPERIMENTS ON THE INHERITANCE OF COAT-COLOUR IN RABBITS.

By R. C. PUNNETT, M.A., F.R.S.

In an earlier paper published in this Journal[1] I gave an account of some experiments with rabbits in which it was shewn that the agouti pattern might in certain cases result from the mating of black with black. Until then all the evidence from mice, rats and guinea pigs, as well as from rabbits, pointed to the relation between agouti and black being a simple Mendelian one in which agouti was dominant. The unexpected appearance of agoutis in litters from black parents led to the framing of a hypothesis which may be briefly recapitulated before giving an account of the further experiments which I have made during the past two years. On that hypothesis I suggested that we were dealing with three factors, viz.:

A, the agouti factor which inhibits the full production of black pigment, turning black into agouti, and tortoise into yellow;

E, a factor for the extension of the melanic pigment which turns yellow into agouti and tortoise into black; and

D, a factor which inhibits the operation of the agouti factor, causing the animal to appear almost or quite black even if the agouti factor be present.

In order to explain the experimental results it was suggested that complete coupling occurs between the factors D and E, so that animals of the constitution DdEe produce only the gametes DE and de. The

factor **A** however behaves in segregation independently of **D** and **E**. Owing to this coupling no animal contains **D** unless it also contains **E**, and no animal which is heterozygous for **E** can be homozygous for **D**. In other words, if the coupling is complete, animals of the constitution **DDee**, **Ddee**, and **DDEe** should not be found.

The presence or absence of **D** makes no difference in the appearance of a rabbit which contains **E**, but lacks the agouti factor, **A**. Whether **D** is present or not such animals are normal blacks. But when **A** is present in animals homozygous for **E** their appearance differs according as they are homozygous or heterozygous for **D**. When heterozygous the animal is mainly black with a slight sprinkling of agouti hairs, which are most numerous at the back of the neck (cf. *Journ. Gen.* 1912, Pl. XII, fig. 2); when homozygous it must be supposed to be full black[1]. Further, the appearance of an animal containing both **D** and **A** differs according as it is homozygous or heterozygous for **E**. If homozygous it is an agouti-black: if heterozygous it is a normal black in appearance.

Hence the zygotic constitutions of animals containing **D**, **E**, and **A** are limited to the following:

1. **DDEEAA** }
2. **DDEEAa** } normal black.

3. **DdEEAA** }
4. **DdEEAa** } agouti-black.

5. **DdEeAA** }
6. **DdEeAa** } normal black.

At the time when the earlier results were given in 1912, all of the above six classes had been experimentally identified with the exception of the first. As the identification of these different classes is critical for the hypothesis adopted, experiments were begun in order to find the animal of the constitution **DDEEAA**. It was shewn that when agouti-blacks of the constitution **DdEEAa** were bred together they gave, as the hypothesis demanded, blacks, agouti-blacks, and agoutis closely in the ratio $7:6:3$. Such animals produce the four types of gamete, **DEA**, **DEa**, **dEA**, **dEa**, and the results of two such gametic series meeting is shewn in the subjoined scheme:

[1] Critical evidence in favour of this view was lacking in 1912 but has since been obtained (p. 39).

DEA DEA Black	DEA DEa Black	DEA dEA Agouti-black	DEA dEa Agouti-black
DEa DEA Black	DEa DEa Black	DEa dEA Agouti-black	DEa dEa Black
dEA DEA Agouti-black	dEA DEa Agouti-black	dEA dEA Agouti	dEA dEa Agouti
dEa DEA Agouti-black	dEa DEa Black	dEa dEA Agouti	dEa dEa Black

Fig. 1.

As indicated in the scheme, the 7 blacks should be zygotically of five different sorts, viz.:

1 DDEEAA.
2 DDEEAa.
1 DDEEaa.
2 DdEEaa.
1 ddEEaa.

Crossed with an animal of the constitution **ddEEaa**, the last three classes should give only blacks; those of the constitution **DDEEAa** should give equal numbers of blacks and agouti-blacks; while those of the constitution **DDEEAA** should give agouti-blacks only. The three different classes as revealed by this test should be in the proportion 4:2:1. Moreover no agouti should make its appearance in any of these crosses.

Blacks resulting from the matings between agouti-blacks of the constitution **DdEEAa** were accordingly saved and tested by crossing with the chocolate buck whose history was given in the earlier account (*Journ. Gen.* 1912, p. 233). With respect to the factors in question he was of the constitution **ddEEaa**.

In all, 14 does were tested in this way and gave the results shewn in Table I.

The results tally closely with expectation which demands that the three classes should be found in the ratio 4:2:1. The actual numbers, 8:5:1, are not far removed from the expected 8:4:2. Moreover the case of *F* 238 shews that the animal of the constitution **DDEEAA** is

TABLE I.

Blacks ex agouti-black × agouti-black.

F 188 × choc. gave	4 black				
F 189 ,, ,,	2 ,,				
F 190 ,, ,,	7 ,,				DDaa
F 194 ,, ,,	6 ,,				Ddaa
F 198 ,, ,,	6 ,,				ddaa
F 199 ,, ,,	4 ,,				
F 212 ,, ,,	3 ,,				
F 213 ,, ,,	5 ,,				
F 93 ,, ,,	4 black + 5 agouti-black				
F 94 ,, ,,	4 ,, + 1 ,,				
F 207 ,, ,,	1 ,, + 1 ,,				DDAa
F 215 ,, ,,	1 ,, + 2 ,,				
F 217 ,, ,,	4 ,, + 2 ,,				
F 238 ,, ,,	10 agouti-black				DDAA

a normal black in appearance. This deduction, which could only be assumed in the earlier account (*Journ. Gen.* 1912, p. 230), is now confirmed by direct experiment.

It was previously pointed out that agouti-blacks must, on the hypothesis put forward, be always heterozygous for **D**. In addition to the eight F_2 rabbits already tested and shewn to fulfil this condition (*Journ. Gen.* 1912, p. 233), five F_3 agouti-blacks (*F* 84, *F* 85, *F* 94, *F* 104, and *F* 150) from agouti-black parents have also been tested. In each instance the animal was shewn to contain **A** and to be heterozygous for **D**.

These further results all served to confirm the view previously advanced, and the chief remaining point of interest was to determine whether the coupling between the factors **D** and **E** must be regarded as complete, or whether it is of the nature of a partial coupling of high intensity. For this purpose a number of rabbits of the constitution **DdEeAA** were bred (see *Journ. Gen.* 1912, p. 233) and mated with animals containing neither **D** nor **E**. The appearance of a few agoutis from such matings would indicate that the coupling was partial. The facts obtained are shewn in Tables II and III[1].

Some further data are also given from the matings of four does of the constitution **DdEeAa** (Table IV). If the coupling between

[1] A few of the data given in Tables II—IV have already been recorded (*Journ. Gen.* 1912, pp. 233, 234). The bulk of them however are new.

D and E is partial, agoutis are also to be expected here, though of course the chance of their appearing is only half as great as in the case of animals which are homozygous for A.

As these Tables shew, 476 rabbits in all have been bred from animals of the constitution DdEe (which also contain A) when mated

TABLE II.

		♂ E 31 (ddeeAa)		♂ F 235 (ddeeAA)		Orange ♂ (ddeeaa)		♂ 74 (ddeeaa)		♂ G 35 (ddeeAA)		Totals	
		blk	yell.	blk	yell	blk	yell	blk	yell.	blk	yell.	blk	yell.
	F 63	2	2	2	8	2	3	1	2	—	—	7	15
	F 67	5	2	9	10	—	—	—	—	—	—	14	12
DdEeAA ♀♀	F 118	2	4	8	8	—	—	—	—	1	1	11	13
	F 231	—	—	2	2	5	2	—	—	—	—	7	4
	F 232	—	—	5	8	2	2	—	—	2	3	9	13
	F 233	—	—	5	1	2	4	3	2	—	—	10	7
	G 20	—	—	—	—	—	—	—	—	3	1	3	1
										Totals		61	65

TABLE III.

		♂ ♂ DdEeAA							
		♂ F 51		♂ F 20		♂ G 12		♂ G 21	
		blk	yell	blk	yell	blk	yell.	blk	yell
	♂ ddee	7	3	2	3	—	—	—	—
F 128	,,	—	—	3	2	5	10	—	—
F 222	,,	—	—	—	—	—	—	6	1
F 223	,,	—	—	3	0	3	7	8	9
F 230	,,	—	—	2	4	—	—	—	—
F 236	,,	—	—	—	—	2	1	2	6
G 17	,,	—	—	—	—	6	5	7	9
G 18	,,	—	—	0	2	6	8	6	1
G 19	,,	—	—	3	6	1	2	1	1
G 22	,,	—	—	—	—	4	3	6	6
G 23	,,	—	—	—	—	4	1	9	8
G 30	,,	—	—	—	—	8	10	—	—
G 41	,,	—	—	—	—	—	—	4	5
G 42	,,	—	—	—	—	3	2	1	5
G 43	,,	—	—	—	—	8	8	—	—
G 49	,,	—	—	1	0	—	—	—	—
		7	3	14	11	17	57	50	54

Totals { Black 118
{ Yellow 125

TABLE IV.

		♂ E 31 (ddeeAa)			♂ (ddeeaa)			♂ F 235 (ddeeAA)	
		blk.	yell	tort.	blk.	yell.	tort	blk.	yell.
F 22	♀ DdEeAa	7	5	2	10	10	8	4	2
F 62	,,	3	1	1	4	2	3	3	2
F 66	,,	3	2	1	2	1	2	—	—
F 69	,,	3	6	3	9	4	4	—	—.
	Totals ...	16	14	7	25	17	17	7	4

with animals of the constitution **ddee**. Since no agouti has appeared it must be inferred that **dEA** gametes (and also **Dea** gametes) were not formed. Hence it must be supposed that the coupling between **D** and **E** is complete, or that if partial, it is of very high intensity. At present we have no grounds for supposing that it is not complete.

The Chocolate Series.

In my earlier paper I gave a brief account of some experiments with a chocolate rabbit, for which I was indebted to the kindness of Dr Hagedoorn (*loc. cit.*, p. 235). Further work has confirmed the view that chocolate in the rabbit, as in the mouse, behaves as a simple recessive to black, and that the black series of colours is paralleled by a corresponding recessive chocolate series. Chocolate × yellow gives agoutis in F_1, and these agoutis bred together give in F_2 agouti, black, yellow and tortoise, and also cinnamon, chocolate, dilute cinnamon, and orange—the corresponding colours in the chocolate series. The considerable mass of data accumulated during the past few years amply confirms the view that the chocolate series runs strictly parallel with the black series, differing from the latter simply in lacking the factor for black (**B**).

The relations of the chocolate series to the factor **D** are however of interest, and may be considered in more detail. A pedigree is given in Fig. 2 in order that the somewhat complicated experiments may be more easily followed. An F_2 agouti-black doe of the constitution **DdEEAa** was mated with the chocolate buck received from Dr Hagedoorn. Since her gametic output is **DEA, DEa, dEA, dEa**, she gave, as was expected, blacks, agoutis, and agouti-blacks, all of which were of course heterozygous for **B**. The blacks and agoutis

were indistinguishable from the corresponding colours which are homozygous for **B**. But the agouti-blacks heterozygous for **B** are in appearance quite distinct from those that are homozygous. The agouti hairs are very much more marked and spread throughout the coat (cf. Punnett, 1912, Pl. XII, figs. 1 and 2). Such rabbits are in constitution **DdEEAaBb**. Additional animals of like appearance and
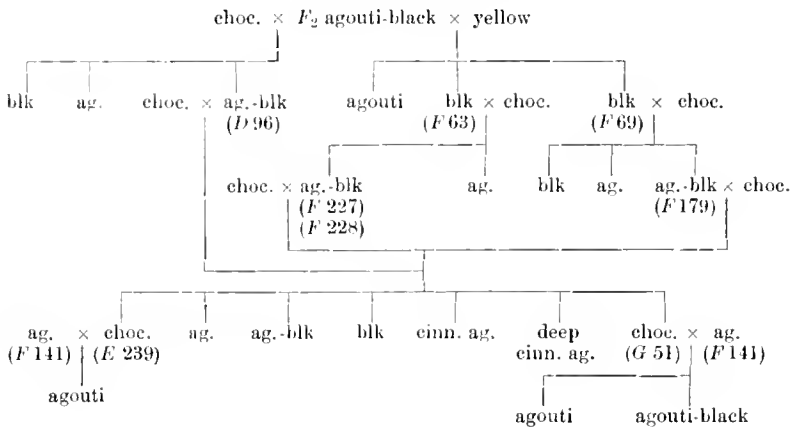
Fig. 2.

constitution were made by mating the chocolate buck with two agouti-throwing black ♀ ♀ (F 63 and F 69) ex F_2 agouti-black × yellow (cf. Fig. 2). Four agouti-black ♀ ♀, all of which were heterozygous for **B** (D 96, F 179, F 227, and F 228 in Fig. 2), were then mated back with the chocolate buck. As shewn in Table V they produced young of 6 kinds, viz. agouti, agouti-black[1], and black, together with the corresponding chocolate forms, cinnamon, deep cinnamon, and chocolate.

TABLE V.

	Agouti	Agouti Black	Black	Cinnamon	Deep Cinnamon	Chocolate
D 96	3	3	4	2	2	4
F 179	4	1	5	4	3	8
F 227	5	3	5	1	2	6
F 228	—	1	5	1	2	3
Totals	12	8	19	8	9	21
Expect.	9·6	9·6	19·2	9·6	9·6	19·2

[1] These were all of the type which previous experience has shewn to be heterozygous for chocolate.

Moreover the proportion in which these 6 forms occurred is that expected on hypothesis. The agouti-black ♀ ♀ of the constitution **DdEEAaBb** must be supposed to produce 8 kinds of gamete—**DEAB**, **DEAb**, **DEaB**, **DEab**, **dEAB**, **dEAb**, **dEaB**, **dEab**—while all of the gametes of the chocolate ♂ are of the type **dEab**. The result of such a cross is shewn in Fig. 3, and, as Table V indicates, the expectation of the 6 classes in the ratio 1 agouti, 1 agouti-black, 2 black, 1 cinnamon, 1 deep cinnamon, 2 chocolate is closely realised in fact.

DEAB	DEAb	DEaB	DEab
dEab	dEab	dEab	dEab
Agouti-black	Dark Cinnamon	Black	Chocolate
dEAB	dEAb	dEaB	dEab
dEab	dEab	dEab	dEab
Agouti	Cinnamon	Black	Chocolate

Fig. 3.

It is evident from Fig. 3 that the chocolates (as also the blacks) produced should be of 2 sorts, viz. those heterozygous for **D**, and those which do not contain this factor. In order to put this to the test two of these chocolates were mated with a homozygous agouti ♂ (*F* 141)[1]. One of these chocolates (*E* 239) gave 9 agouti young and was therefore of the constitution **ddEEaabb**. The other (*G* 51) produced 2 agoutis and 2 agouti-blacks. Her constitution must therefore have been **DdEEaabb**. The experiment establishes the fact that an animal which is pure chocolate in appearance can carry the factor **D**. All the evidence shews that there exists a chocolate series containing the factor **D** which is strictly parallel to the corresponding black series.

Here mention may be made of a few experiments which I carried out with blue rabbits, from which it is clear that a blue rabbit may carry the factor **D** in the same manner as a black. Thus a blue doe (*F* 211) was made which, when crossed with the original chocolate buck (cf. p. 42), gave 2 blacks, 1 agouti-black, and 1 agouti. Evidently the absence of the factor which turns blue into black does not affect the relations of the factor **D**.

[1] With 2 chocolate ♀ ♀ this buck gave 16 agouti young, with a chocolate Himalayan he gave 6 agoutis, and with an orange (= dilute chocolate) doe he gave 9 agoutis. No offspring of any other colour were produced and there can therefore be no doubt that in constitution he was **ddEEAABB**.

Discussion.

From the preceding account it is clear that all the facts observed in this series of experiments can be interpreted on the "Presence and Absence" hypothesis if it be supposed that complete coupling obtains between the factors **D** and **E**. There is however another hypothesis—that of "Multiple Allelomorphs"—which has been put forward in connection with this and similar cases[1]. The difference between the two explanations may best be brought out by considering the instance used by Sturtevant (10) in a recent discussion of the problem. It was pointed out some years ago by Hurst and by Castle that albinism behaves as a simple recessive to self-colour. Both of these observers have further shewn that the Himalayan pattern also behaves as a simple recessive to self-colour. Castle's experiments again proved that the Himalayan pattern is a simple dominant to albinism. Nevertheless Himalayans do not appear in F_2 families from self-colour × albino. Sturtevant has pointed out that the genetic behaviour of these colour varieties is covered by either of two hypotheses.

A. On the "Presence and Absence" hypothesis we must suppose that two factors are concerned, viz. **C**, a colour producer which is present in the self-coloured and in the Himalayan rabbit, and **S**, a factor which turns the Himalayan into self-colour. Zygotically therefore the three forms may be represented thus:

Self-coloured	...	**CCSS**,
Himalayan	...	**CCss**,
Albino ...	...	**ccss**.

The albino must be supposed to lack **S** because no case is known of a self-coloured rabbit being produced from the mating Himalayan × albino.

In order to account for the non-appearance of Himalayans in F_2 from self-colour × albino, we must suppose that there is complete coupling between **C** and **S**, so that F_1 rabbits of the constitution **CcSs** produce only gametes of the form **CS** and **cs**.

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[1] The hypothesis would appear to have been put forward independently by Morgan (7) and by Wilson (12) in 1913 (see also note on p. 46).

B.   On the "Multiple Allelomorph" hypothesis it must be supposed
that we are dealing with three definite factors, any one of
which is allelomorphic to any other, so that a given zygote
cannot contain more than two of the three. If, following
Sturtevant, we denote these factors as **S**, **H**, and **A**, the
zygotic constitution of the three varieties becomes:

Self-coloured   ...   **SS,**
Himalayan   ...   ...   **HH,**
Albino   ...   ...   **AA.**

The heterozygous self-colour which throws Himalayans is
SH, and that throwing albinos is **SA**: while **HA** represents
the constitution of a Himalayan which throws albinos[1].

It is clear that either hypothesis will cover all the facts. It is
equally clear that the "Multiple Allelomorph" hypothesis carries with
it the abandonment of the "Presence and Absence" hypothesis, not
only in such cases as the present, but in all cases where Mendelian
inheritance has been shewn to hold good. For there would appear to
be no reconciliation possible between a hypothesis which interprets
characters behaving as alternate in heredity, in terms of factors which
are alternative in the gamete, and one in which an alternate pair of
characters is interpreted in terms of the presence or absence of a single
factor. In attempting to decide which of the two views is to be pre-
ferred, the rabbit case dealt with in the earlier part of this paper is
not without interest.

In Sturtevant's discussion of the matter he points out that in these
cases, where a given character appears to act as a simple dominant to
two different recessives, and where one of these recessives also behaves
as a simple dominant to the other, the three characters concerned are
closely related physiologically. From this he argues that a given
factor is a complex thing which may undergo modifications affecting
its manifestation in the zygote without at the same time affecting its
allelomorphic distribution in gametogenesis. In the rabbit case for
example the factor for self-colour, which we may denote by **X**, is
normally allelomorphic to itself. As the result of some unknown
change in the constitution of the factor it loses the property of

[1] Wilson (1913) has also advocated the hypothesis of Multiple Allelomorphs in con-
nection with the Agouti-black rabbit. On his interpretation the factor **X** (= **DE**) always
turns a rabbit into a black or an agouti-black. This however is not in accordance with
fact, since the factor in question can be carried by a chocolate (cf. p. 44).

bringing about complete pigmentation, passing into the condition X′, so that animals which are homozygous for the factor after the change has occurred (X′X′) display the Himalayan pattern in place of self-colour. Again, as the result of some other unknown change it becomes X″ and loses the property of bringing about any pigmentation, so that animals homozygous for the factor in this condition (X″X″) are albinos. Nevertheless both X′ and X″ remain equivalent to X and to one another in the mechanism of factorial distribution, i.e. any one of the three is allelomorphic to any other one[1].

Of the cases cited by Sturtevant in support of his contention three, viz. the Himalayan rabbit case, the case of the green, variegated, and *chlorina* foliage in *Aquilegia*, and that of the red, eosin, and white eye in *Drosophila*, are certainly favourable to it. In all of them there is a series of three forms of diminishing pigmentation, and the genetic relations are similar in all[2].

In this connection the rabbit case dealt with in the earlier part of this paper is of interest, as it differs in some respects from the group of cases just mentioned. On the presence and absence hypothesis the two factors D and E are, so far as is known, completely coupled, and the three gametic possibilities are therefore DE, dE, and de. To bring this case into line with those discussed above we should have to refer these three possibilities respectively to the three allelomorphs X, X′, and X″. The subjoined table represents the zygotic formulae of the various possible combinations on these two hypotheses, both when the agouti factor is present and when it is absent.

Without the agouti factor			With the agouti factor		
DDEE	black	XX	DDEEAA	black	XXAA
ddEE	black	X′X′	ddEEAA	agouti	X′X′AA
ddee	tortoise	X″X″	ddeeAA	yellow	X″X″AA
DdEE	black	XX′	DdEEAA	agouti-black	XX′AA
DdEe	black	XX″	DdEeAA	black	XX″AA
ddEe	black	X′X″	ddEeAA	agouti	X′X″AA

[1] Sturtevant does not suggest what the nature of these changes in the factor may be—whether some internal change involving merely a rearrangement of its constituents and analogous to isomerism in chemistry, or the definite loss of some constituent in each case. The latter view would practically mean the application of the presence and absence hypothesis to certain of the constituents of the factor itself.

[2] The case of Emerson's beans also cited by Sturtevant may perhaps be of a similar nature, but until the relation of the green-leaved-yellow-podded to the yellow-leaved-yellow-podded form has been investigated this cannot be regarded as certain.

When the agouti factor is present the three homozygous forms XX, X′X′, X″X″ form what may be regarded as a series of diminishing intensity for the melanic pigment, viz. black, agouti, yellow. In the absence of the agouti factor the series is black, black, tortoise. Though the first term is now in appearance indistinguishable from the middle one, it is theoretically possible to regard it as potentially of a more intense black, the difference between the two being rendered visible when A is inserted as an indicator. So far the manifestation of pigment is not at variance with the view that the three allelomorphs X, X′ and X″ form a series of diminishing intensity. A difficulty however arises when we come to consider certain of the heterozygous forms. XX′AA is agouti-black, and since X′ must be regarded as a factor for higher pigment intensity than X″ we should expect XX″AA to shew less intensity of melanic pigment than XX′AA. It should be something lighter than agouti-black, whereas it is actually full black. We cannot therefore regard the factors X, X′, and X″ in this case as forming a series of diminishing intensity for melanic pigmentation, and Sturtevant's argument, applicable in the cases of the Himalayan rabbit, the eye-colour of *Drosophila*, and the variegated *Aquilegia*, here falls to the ground.

Apart from the difficulty of interpreting the experiments dealing with the D factor in rabbits in terms of the "Multiple Allelomorph" hypothesis, there seem to me to be other reasons for treating all of these cases as examples of complete coupling and retaining the interpretation in terms of the "Presence and Absence" hypothesis. In this connection some recent work of Tanaka on silkworms is much to the point. In his account of the inheritance of the two larval characters striping (S) and yellow (Y) as opposed to non-striping (s) and white (y), Tanaka shews that the experimental data can only be interpreted on the supposition that there is partial coupling in the male gametes and complete coupling in the female gametes. The male gametic series is of the form 3SY : 1Sy : 1sY : 3sy (or 2SY : 1Sy : 1sY : 2sy), while the female series is of the form SY : sy. Unless we are to suppose that the hereditary mechanism is of a different order in the two sexes, we can scarcely avoid the conclusion that the complete coupling exhibited in the female is but a particular form of the partial coupling found in the male series of gametes. And if we accept the hypothesis of complete coupling in this case it seems not unreasonable to extend it to other cases where partial coupling for the factors concerned is hitherto unknown.

Nor should it be forgotten that more ample data may shew these debatable cases to be examples of partial coupling of very high intensity. The appearance of a single Himalayan in F_2 from the cross of self-colour × albino of an eosin-eyed *Drosophila* ex red eye × white would, as Sturtevant admits, invalidate the "Multiple Allelomorph" hypothesis. Cases are now known where the coupling between two factors, though not quite complete, is of very high intensity. In sweet peas for example the coupling between the factor for blue (**B**) and that for the erect standard (**E**) is such that in plants heterozygous for both factors, the gametic series must be supposed to be 127**BE** : 1**Be** : 1**bE** : 127**be**. Such plants crossed with **be** pollen would give but a single specimen of each of the two rarer classes (blue hood and red erect) in 256 plants. If the coupling were of even higher intensity it might easily be regarded as complete unless very large numbers were raised. As time goes on the phenomenon of partial coupling and repulsion is turning out to be a widely spread one among animals as well as plants. Whatever the explanation may turn out to be ultimately, it seems reasonable to regard cases of apparent complete coupling as falling into the general scheme until we have definite evidence to the contrary. It would appear premature therefore to reject the "Presence and Absence" hypothesis for that of "Multiple Allelomorphs" until we are in possession of facts which compel us to take this step. We certainly do not possess such facts at present.

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HEREDITARY SYNDACTYLISM AND POLYDACTYLISM.

By J. S. MANSON, M.D.

In the study of human genetics digital abnormalities present special features as compared with other hereditary abnormalities. As a rule the condition of digital abnormality is so self-evident that it cannot be mistaken even by an unobservant mind for anything else. Again, affected persons are somewhat proud of this condition, or at least make no attempt at its concealment, so that when it appears in a family the members are usually well informed as to their affected and unaffected relatives even for one or more generations back. This is a great advantage to the investigator in human heredity because he has to rely so much on personal statements and memories regarding the condition of distant and dead relatives. Thus, personal statements regarding the presence or absence of digital abnormality have a greater degree of accuracy than similar statements regarding other human hereditary abnormalities such as those of the eye, skin, etc., which require special skill for their diagnosis from acquired conditions.

The family described in this article originated from one William Joseph who was born and lived at Aberystwith in Wales about the beginning of the 19th century. This man was affected with webbing of the 3rd and 4th fingers on the hands, and had 6 toes on each foot.

In the accompanying pedigree 64 descendants are shown of whom 27 are affected, 33 unaffected, and 4 doubtful.

The chief branches of the family live in Warrington, Widnes and Salford, and all those alive in these places with the exception of 3 have been seen and examined by the writer, and two photographs of the remaining 39 have been seen, leaving the condition of 37 to be based on the statements of the writer's informants who are themselves members of the 3rd generation.
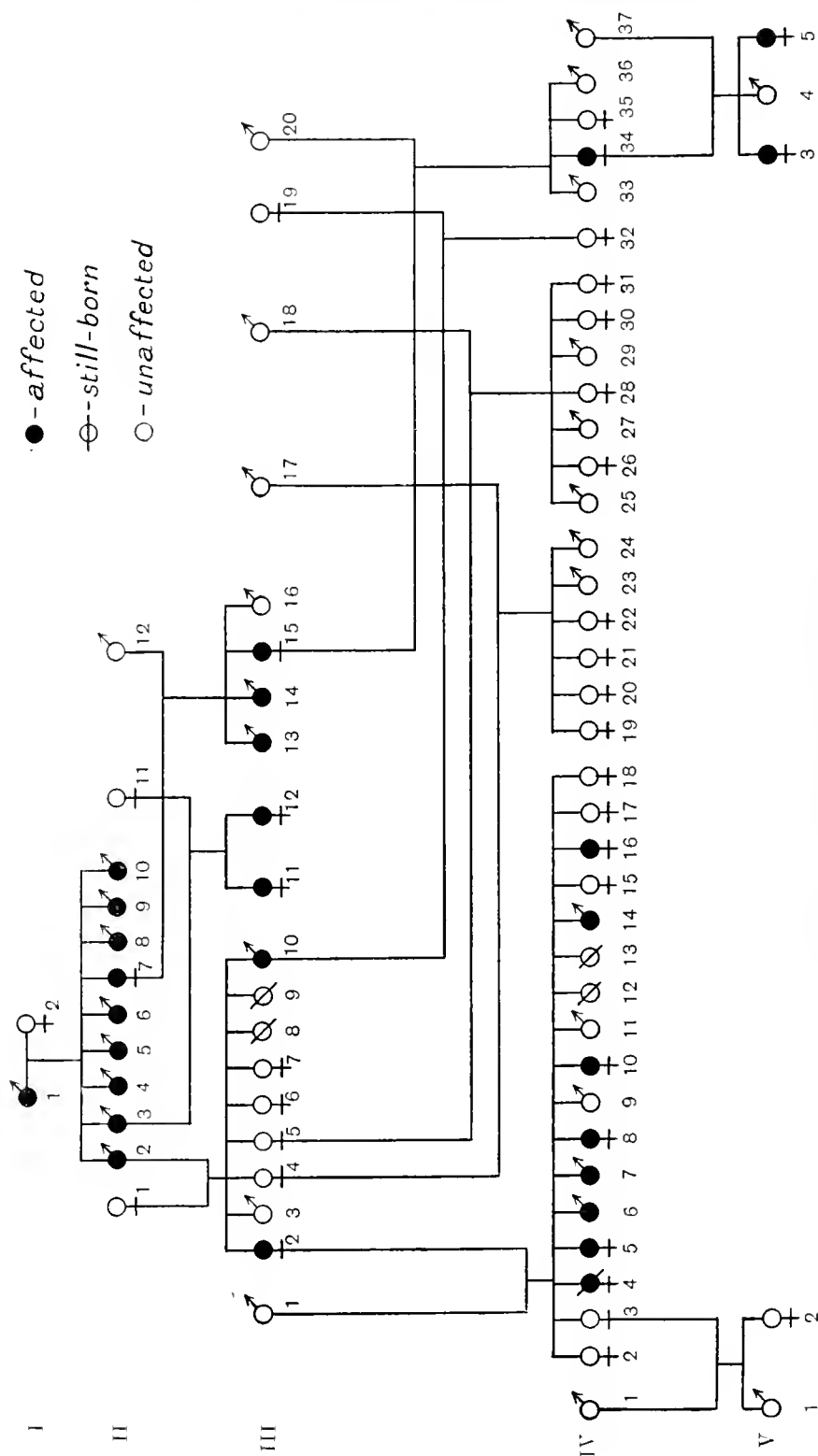
Hereditary Syndactylism and Polydactylism.

Only the Warrington and Salford branches of the family are affected; the Widnes branches are unaffected. There are four photographs which show the external condition in three generations of the Warrington family, and in addition there are eight skiagraphs of the hands and feet of the living affected members of this branch.

Five skiagraphs of the hands and feet of the affected members of the Salford family were also obtained, and all will be referred to in the description of the several members composing the pedigree. At the outset it may be mentioned that while externally the polydactylism which affects the feet is evident by the existence of an extra toe in some of the members, the real condition of the hands cannot be realized without the aid of the skiagraphs. The latter show that in the hands also there is a condition of aborted or suppressed polydactylism which must have some real significance in relation to the condition of the feet.

Description of Members of Pedigrees.

In describing the members of the pedigree the numbers on the diagram will be used to identify the person or persons described. The Roman numerals refer to the generation, and the Arabic numerals to the serial order in that generation.

Generation I.

I. 1. William Joseph, born at Aberystwith in Wales about the beginning of the 19th century and lived there all his days, occupation tailor. He had webbed 3rd and 4th fingers on each hand, and 6 toes on each foot. He once made a short visit to Warrington to see his son II. 2, and the writer's chief informant III. 2 has distinct memories from early girlhood of the condition of his hands.

By his wife I. 2 he had 8 sons and 1 daughter II. 2—II. 10.

I. 2. No definite information except that it is believed that she had normal hands and feet.

Generation II.

II. 2—II. 10 issue of I. 1 and I. 2 and all were affected with webbed 3rd and 4th fingers in each hand, and 6 toes on each foot.

II. 2. William Joseph, eldest son of I. 1, came to Warrington about 1840 and worked as a cabinet maker. He died in 1895. Was married twice, no issue by first wife (not shown on pedigree); by second wife Mary Jane Opie II. 1 who was unaffected had issue III. 2—III. 10.

The 3rd and 4th fingers on each hand were webbed. He also had 6 toes on each foot, the 4th, 5th, 6th toes being webbed. These were seen by his daughter III. 2—the writer's chief informant.

II. 3. David lived at Aberystwith, married II. 11, who was unaffected as far as is known. He had, like his father, webbed 3rd and 4th fingers on both hands, 6 toes on each foot. Issue III. 11, III. 12 both affected: degree unknown.

II. 7. Elizabeth lived with her brother II. 2 in Warrington until she married II. 12, Jones, had issue III. 13—III. 16. She was affected in a similar manner to her brother and father.

II. 4, 5, 6, 8, 9, 10 were all affected with webbed 3rd and 4th fingers on each hand, and 6 toes on each foot. The writer's chief informant is very positive on this although she cannot give any further information regarding these six uncles. Naturally the reader may have some doubts regarding the uniformity of the condition in this second generation, but the writer is compelled to state the information as he received it, and considerable reliance must be placed on III. 2's statements because her information regarding the Salford family, which was only discovered after a considerable search, proved accurate.

Generation III.

III. 2. Charlotte Joseph married III. 1 (Oliver) unaffected: lives in Warrington. Had issue IV. 2—IV. 18, condition of hands and feet shown on Plate XIV where she is photographed with her daughter Charlotte IV. 8. The webbing of the 3rd and 4th fingers on each hand is well shown, and the marked crooking of the two webbed fingers on the left hand is very evident. It will be noted in addition that there is a crooking of both little fingers.

In the feet the right foot shows 6 toes with webbing of 4th, 5th, 6th. The left foot is normal.

Skiagraph B (Plate XV) shows the condition of the bones in the hands.

Right Hand. As in the photograph the webbing and union of the soft parts are seen but the metacarpal bones and phalanges are distinct. It will be seen that the terminal phalanx of the 4th finger has the appearance of being composed of the union of two phalanges, leaving a distinct foramen in the centre of the union. The little finger is distinctly crooked.

Sesamoid bones are present at the metacarpo-phalangeal joints of thumb, index, and little finger.

Left Hand. The marked deformity of the webbed 3rd and 4th fingers is well seen on Plate XV, and the explanation of this deformity is at once evident from the condition of the bones shown in the Skiagraph. This shows that the terminal and middle bony phalanges of the 3rd finger are shortened and joined to form one bone which articulates with the head of a proximal normal phalanx.

The 4th finger shows a remarkable bony formation. Its proximal phalanx is made up of an irregular mass of bone unlike a normal phalanx. The aspect of this bone adjacent to the little finger resembles that of a normal phalanx, but the aspect next to its webbed fellow is quite irregular. The distal aspect of this bone forms a $\big)$ shaped surface in which articulates an irregularly shaped middle phalanx. The distal phalanx is shorter than normal; the little finger is crooked. Sesamoid bones are present at the metacarpo-phalangeal joints of the 2nd, 3rd and 4th fingers as well as at the thumb and little fingers.

Skiagraph B₁ (Plate XVI). *Right Foot* shows the bony condition of the 6 toes. The abnormal features are the 5th and 6th incomplete metatarsals and the bony formation of the 5th and 6th toes. The 5th metatarsal arises from the base of the 4th metatarsal and has no tarsal articulation, but has a complete head which articulates with the base of the two conjoined proximal phalanges of the 5th and 6th digits. The 6th metatarsal has no articulating head but has a complete tarsal articulation with the cuboid. The bones of the 5th and 6th toes are formed by a proximal bone which has a single base articulating with the 5th metatarsal, and arising from this are two distinct and separate heads which articulate with two irregularly shaped distal phalanges, having pointed extremities. The peculiar bony condition of this part should be well marked, for a very similar condition appears in other members of this pedigree.

Left Foot. The bony condition is practically normal except the marked crooking of the 4th and 5th toes, which is probably an acquired condition from boot pressure.

III. 3. William, unaffected, dead.

III. 4. Ellen, unaffected, married III. 17, had issue IV. 19—24, lives at Widnes.

III. 5. Sarah, unaffected, married III. 18 (Oliver), brother of III. 1, had issue IV. 25—31, lives at Widnes.

III. 6, 7, unaffected.

III. 8, 9. Still-born, condition doubtful.

III. 10.   Alfred, affected, webbed fingers on both hands, and 6 toes on each foot.   Married III. 19, died a year or so after marriage, issue IV. 32.

III. 11, 12, affected, webbed fingers and extra toes.

III. 13.   Elias Jones, affected, married, no issue.

III. 14.   Alfred, affected, supposed to be living in Manchester, issue unknown.

III. 16.   David, unaffected, dead.

III. 15.   Elizabeth, married III. 20 (Foster), lives in Salford, issue IV. 33—36.   Has webbed 3rd and 4th fingers on each hand, the right hand being markedly deformed, and 6 toes on each foot, 4th, 5th, 6th being webbed.

Right Hand.   The bony phalanges of the 3rd finger are normal in length and shape, but the terminal phalanx is bent towards the 4th finger at almost a right angle, and there it unites with terminal phalanx of its webbed fellow forming a bony union.   The 4th meta-carpal is much shorter than its fellows.   The proximal phalanx of the 4th finger is also shorter than normal, and is very irregular in shape, having a bony process projecting towards the head of the 3rd metacarpal. The middle phalanx is normal in shape and size, while the terminal phalanx is short, and joined by bony union to the terminal phalanx of the 3rd finger.   Sesamoid bones present at 1st, 3rd and 5th meta-carpo-phalangeal joints.

Left Hand.   The abnormal bony features are similar to those on the right hand but much less in degree.   The terminal phalanx of the 3rd finger is bent towards that of the 4th, and there fuses with it, forming a bony union which is so far incomplete as to leave a foramen in the centre of the union.   The other principal abnormal feature is the misshapen proximal phalanx of the 4th finger which has a small bony process projecting towards the proximal phalanx of the 3rd finger. Sesamoid bones present only at 1st, 2nd and 5th metacarpo-phalangeal joints.

Right Foot.   This shows an abnormal 5th metatarsal bone having two heads, an articulating head and a non-articulating head.   The articulating head lies to the inner side, and on it rests the articulating base of the 5th proximal phalanx.   This phalanx is made up of a broad base and two heads on which rest two irregularly shaped phalanges of the 5th and 6th toes.

Left Foot.   The abnormal bony condition of this foot resembles that of the right foot with the exception that the bony union between the

articulating and non-articulating heads of the 5th metatarsal is much less complete. In this foot they are almost separate.

Generation IV.

IV. 2, 9, 11, 18. Nellie, Thomas, Alfred, Gladys, unaffected, dead.

IV. 4, 5, 7, 10. Stillborn, Maggie, James, Mabel, affected, dead.

IV. 12, 13. Stillborn, condition unknown.

IV. 3. Mary, unaffected, married IV. 1, Wilford, issue V. 1, 2.

IV. 6. William, webbed 3rd and 4th fingers on both hands; on the right hand the 4th finger is permanently crossed over the dorsum of the 3rd finger. Feet are normal.

Right Hand. The chief abnormal features in the bony formation of this hand are the short and irregularly shaped proximal phalanx of the 4th finger and the process of bone projecting from it towards the head of the 3rd metacarpal bone. This piece of bone resembles a portion of a metacarpal bone and does not seem to form a bony union with the proximal phalanx of the 4th finger. The end towards the head of the 3rd metacarpal seems to push this apart from its fellow the 4th metacarpal. This separation of the metacarpals, together with the junction of skin, are the causes of the marked deformity in this hand. The other phalanges of the 3rd and 4th fingers are normal in shape and size.

Sesamoid bones at 1st, 2nd, 3rd and 5th metacarpo-phalangeal joints.

Left Hand. Here the bony condition is normal, and the abnormality is limited to the skin.

Sesamoid bones 1st, 2nd, 3rd, 4th and 5th metacarpo-phalangeal joints.

IV. 8. Charlotte (see Plate XIV, B). Webbed 3rd and 4th fingers on right hand. Left hand normal; 6 toes on right foot, 4th, 5th, 6th webbed. Left foot apparently normal.

Right Hand shows abnormal and shortened middle phalanx of 4th finger and bony union of extremities of 3rd and 4th terminal phalanges.

Sesamoid bones at 1st, 2nd, 3rd and 5th metacarpo-phalangeal joints.

Left Hand is normal.

Sesamoid bones at 1st, 2nd, 3rd, 4th and 5th metacarpo-phalangeal joints.

Right Foot. The bony condition of this foot so closely resembles that of her mother's described from Skiagraph B₁, that one description will suffice. If anything the abnormal condition here is more pronounced than in the mother.

Left Foot. The skiagraph shows here in an apparently normal foot a detached and anomalous piece of bone, lying in close proximity to the head of the 5th metatarsal bones, otherwise the foot is normal.

IV. 14. Charles (see Plate XIV, D), aged 12. Webbed 3rd and 4th fingers on right hand and 6 toes on each foot, 4th, 5th, 6th webbed with partial webbing of 3rd and 4th toes.

Skiagraph F (Plate XVII). *Right Hand* shows bony abnormalities of the 3rd and 4th fingers. The proximal phalanx of the 4th finger is represented by 3 distinct bones, the larger central bone acting as a phalanx whose proximal end articulates with the 4th metacarpal and distal end with the middle phalanx. There are two lateral bones, the larger lying towards the 5th finger and the smaller towards the 3rd finger.

The middle phalanx of the 4th finger forms a bony union with the head of the proximal phalanx of the 3rd finger and the remaining phalanges of both fingers join in bony union to form practically one bone.

Sesamoid bones not shown in skiagraph.

The middle phalanx of the 5th finger shows a small piece of bone on its dorsal aspect, both fingers are crooked.

Skiagraph F₁ (Plate XVIII). *Right Foot* shows 6 metatarsal bones, the 6th metatarsal bone is almost complete but lacks the rounded articular head. The 5th and 6th proximal phalanges are distinct and separate but have one common epiphysis which articulates with the head of the 5th metatarsal. The 5th, 6th, middle and terminal phalanges are distinct and separate.

Left Foot shows 6 complete metatarsals and phalanges.

IV. 16. Mabel (see Plate XIV). Webbed 3rd and 4th fingers on right hand. Left hand and feet normal.

Right Hand, bones normal.

Left Hand, bones normal.

Sesamoid bones, not shown.

IV. 15, 17. Ivy and Phyllis, unaffected.

IV. 19—24. (Allen) all unaffected.

IV. 25—31. (Oliver) all unaffected.

IV. 32. (Joseph) unaffected.

IV. 33, 35, 36.   Fisher, William, Emily and Alfred, unaffected.

IV. 34.   Margaret Fisher, married IV. 37 (Weir), issue V. 3—5. Has webbed 3rd and 4th fingers on each hand.   The tips of the 3rd and 4th fingers of left hand are more completely joined than those on the right side.   The nail is single in form and appearance except for a dividing line between the two halves.   There are 6 toes on each foot but the 5th toe is very diminutive in size but has a distinct and well-formed nail.

Right Hand, shows that the bony phalanges of the 3rd and 4th fingers are normal in size and shape, but are permanently in touch with each other from the head of the 4th proximal phalanx in a distal direction.   This also shows that the middle phalanx of the 5th finger is shorter than normal.

Sesamoid bones at 1st, 2nd, 3rd, 4th and 5th metacarpo-phalangeal joints.

Left Hand.   Here the proximal and middle phalanges of the 3rd and 4th fingers are normal in shape and size, but the terminal phalanges are bent towards each other and join to form a bony union.

The middle and terminal phalanges of the 5th finger have joined to form one bone.   From what appears to be the limits of the middle phalanx of this 5th finger, it must be judged to be shorter than normal.

Sesamoid bones at 1st, 2nd, 3rd, 4th, 5th metacarpo-phalangeal joints.

Right Foot.   Metatarsals normal in number and shape, and articulating with the head of the 5th metatarsal are two irregularly shaped bones.   The outer of these articulates with an H-shaped bone which represents the bony basis of the 5th and 6th toes.

Left Foot.   Metatarsals normal in number and shape except that from the inner side of the head of the 5th metatarsal a process of bone projects.

Lying on the outer side of the head of the 5th metatarsal is a piece of bone on which rests an irregularly H-shaped piece of bone representing the bony formation of the 5th and 6th toes.

Generation V.

V. 1, 2.   Wilford, unaffected.

V. 4.   Leslie Weir, unaffected, dead.

V. 3.   Mabel Weir.   Died at Salford Hospital from scalds ; had 3rd and 4th fingers of both hands webbed, and had had operations to relieve

the condition; also 6 toes on each foot from which the extra toe had been removed by operation.

V. 5.   Dora, aet. 1 year.   Webbed 3rd and 4th fingers on each hand.   Feet normal.

Skiagraph J (Plate XIX).   *Right Hand.*   Here the phalanges of the 3rd and 4th fingers are normal in shape and size but lying between them are three bones which are evidently the bony basis of an extra digit.   The terminal phalanx of this extra digit is in close association but distinct from the terminal phalanges of the 3rd and 4th fingers. The middle bone lies in close association with the proximal phalanx of the 4th finger and middle phalanx of the 3rd.   The proximal bone is smaller, lies between the heads of the 3rd and 4th metacarpals.   There is crooking of the little finger.

Left Hand.   The phalanges of the 3rd finger are normal in size and shape.   In the 4th finger, the proximal phalanx is represented by triangular-shaped bone, and towards the head of the 4th metacarpal is a distinct centre of ossification.   Between this triangular bone and the proximal phalanx of the 3rd finger and close to its base lies a third piece of bone.

The middle phalanx is normal in shape and size and the terminal phalanx is in association with the middle phalanx of the 3rd finger. The little finger is crooked.   This is probably the most interesting of the series of skiagraphs not only as showing the condition of the deformity in the 5th generation but also giving evidence explaining the deformities in the older relatives.

DISCUSSION.

In this pedigree the digital abnormality, whether it be in the form of syndactyly or polydactyly or both, appears as a dominant.   It only appears in the offspring of an affected parent and either sex may transmit.   The offspring of unaffected parents are always free from it.

In comparing the affected families it will be seen that in only one are all the members affected—II. 2—II. 10.   Now it is more than likely that the mother of this family I. 2 was normal.   Had she been affected the tradition would have been preserved in the family.   If this be assumed then it follows as an inference of strong probability that I. 1 was a pure dominant to the condition and that the offspring of this union were impure dominants *DR* to the condition.   Of course the

numbers are small, yet it is very significant that the whole family should be consecutively and uniformly affected.

The result of the matings of these *DR* members with *RR* normals is shown in the pedigree to number 40 of whom 18 are affected, 18 unaffected and 4 doubtful. These figures accord with what might be expected in a Mendelian ratio, for *DR* and *RR* unions.

The nature of the abnormality seems complex and irregular. In only three of the descendants of II. 7 does the abnormality appear complete in the 4 limbs, and this was in the III. 15, IV. 34 and the great grand-daughter—V. 3. In the descendants of II. 2 one, two, and even three limbs escape, and in the bony abnormality itself there is some variation in the affected members.

The polydactylism in the feet is apparently due to an extra digit interpolated between a normal 4th and 5th digit. In only one of the skiagraphs, F_1, does this extra metatarsal appear to have a tarsal articulation. In the others it distinctly arises either from the base or the shaft of the 4th metatarsal, or is represented by a fragment of bone lying between the 4th and a normal 5th metatarsal having an articulation with the cuboid. In III. 15 this piece of bone has partially or completely fused with the 5th metatarsal and forms its articular head.

In the hand the skiagraphs show a condition of incomplete polydactylism, but it is difficult to decide whether the suppressed extra digit lies between a normal 3rd and 4th digit or between a normal 4th and 5th. Skiagraphs of the right hands of III. 15 and IV. 6 show a fragment of a metacarpal lying between apparently normal 3rd and 4th metacarpals, and Skiagraph J (Plate XIX) of infantile hands tends to confirm the impression that the suppressed or aborted digit lies between a normal 3rd and 4th finger.

On the other hand Skiagraph F (Plate XVII) shows a piece of bone in association with the proximal phalanx of the right 4th digit lying towards the 5th digit. All the skiagraphs show that the 4th digit presents the chief abnormalities of irregularly shaped phalanges, while the phalanges of the 3rd digit are of normal shape. These appearances on both hands and feet suggest that in this family the polydactylism present is due to the partial or complete reduplication of the 4th digit of both hands and feet.

With regard to the syndactyly, skiagraphs of IV. 16 and IV. 6 (left hand) show that the webbing of the fingers occurs without evident bony abnormality. In IV. 14, where the polydactylism of the feet is most complete, webbing is not limited to the 4th, 5th and 6th toes, but

there is also partial webbing between the 3rd and 4th toes. This goes to show that the more complete the bony abnormality the greater the tendency to webbing. It would be a fair assumption in this family at any rate to state that the syndactyly present is not a character separate from the bony abnormality but only a feebler expression of it.

While the four descendants of II. 7 who have been examined show that both sides of the body are equally affected, the five descendants of II. 2 show that the right side is affected twice as often as the left side in the proportion of 8 limbs to 4 limbs. The variability in hereditary deformities of the hands and feet has been noted by other writers. Fotherby(1) in his account of a claw hand and claw foot family states that a female of the 4th generation had 7 fingers on one hand and 6 on the other. Anderson(2) in describing a similar claw hand family points out that "the morbid features were not confined to a suppression of parts. Syndactyly, compensatory hypertrophy, distortion of the articulations and multiplication of parts were also present." J. S. Muir(3) and C. Lucas(4) also describe great variability in hereditary digital deformities.

In the family here described, while there is undoubtedly some degree of variability in the deformity, yet the skiagraphs show clearly that it is the 4th digit of both hands and feet that is consistently affected either by complete or partial reduplication. In the future, X-ray photographs of the hands and feet of affected families will no doubt show that there is a greater uniformity in the nature of these hereditary deformities than has hitherto been supposed.

Dwight(5) has shown that there is considerable variation in the bones of what are regarded as normal hands and feet. He explains that this is due to the persistence of embryonic centres indicating bone which normally disappear or fuse with others. That being so, it is to be expected that an hereditary abnormality such as is present in this family, and which must necessarily appear at the very earliest period of embryonic development, would also undergo certain variations due to absorption and fusion.

It is interesting to observe that in the majority of the affected hands in this family sesamoid bones are present at the second, third and fourth metacarpo-phalangeal joints where they are not usually present in normal hands. As these bones are frequently present in embryonic hands it can be inferred that in these affected hands the processes of absorption are below normal. At an early stage of embryonic development the affected parts in the members of this

D   M. O.   C. O.
Pedigree number IV. 16.   Pedigree number IV. 14.

B   C. O. (Sen.)   C. O. (Jun.)
Pedigree number III. 2.   Pedigree number IV. 8.
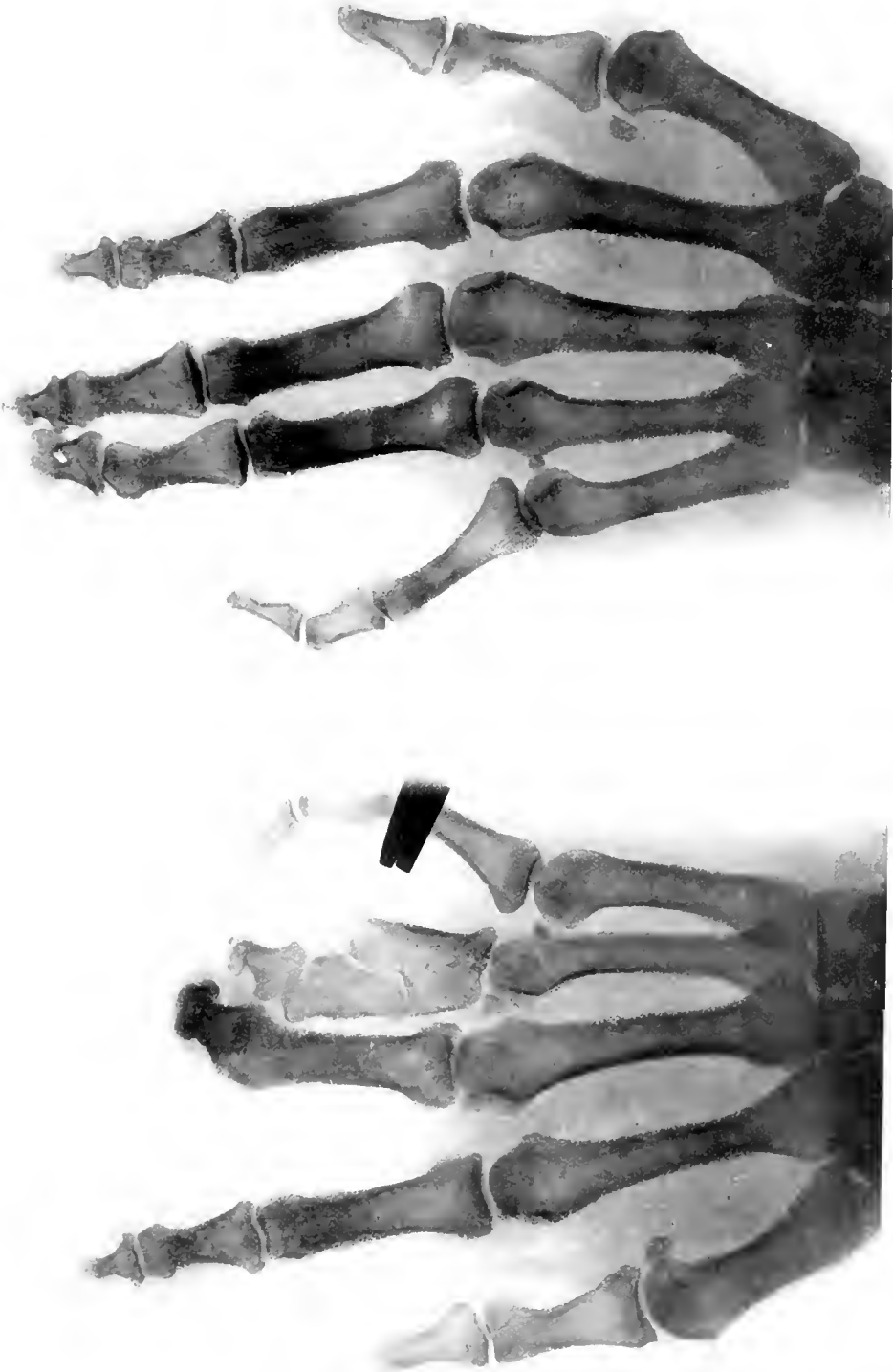
C. C. (S. m.) Pedigree number III, 2.

B

Left

Right

PLATE XVI

Left

Right

C. O. (8·m.) Pedigree number III. 2.

B

Left

Right

C. O. Pedigree number IV. 14.

F

Left

Right

C. o. Pedigree number IV. 14.

F

Left

Right

J

D. W. Pedigree number V. 5.

family would present a more uniform character than they do later when development and differentiation have progressed, and it is this fairly uniform character affecting the 4th digit of both hands and feet which has been transmitted in the manner shown in the pedigree.

The whole series of photographs and skiagraphs have been deposited by the kind permission of Professor Arthur Robinson at the Anatomical Museum of the University of Edinburgh, where they may be seen by anyone interested.

I am greatly indebted to Dr Fox of Warrington for the skiagraphs of the Warrington family and to Dr Barclay of Manchester for the skiagraphs of the Salford family.

EXPLANATION OF PLATES XIV—XIX.

(The numbers refer to the pedigree on p. 52).

PLATE XIV.

Photographs of III. 2, IV. 8 (on block B), IV. 14, and IV. 16 (on block D).

PLATE XV.

Skiagraphs (B) of hands of III. 2.

PLATE XVI.

Skiagraphs (B_1) of feet of III. 2.

PLATE XVII.

Skiagraphs (F) of hands of IV. 11.

PLATE XVIII.

Skiagraphs (F_1) of feet of IV. 11.

PLATE XIX.

Skiagraphs (J) of hands of V. 5.

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5. DWIGHT. *Variations of the Bones of the Hand and Foot*, 1907.

CONTENTS

ON THE STERILITY OF THE TORTOISE-SHELL TOM CAT.

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In a note by one of us in the *Proceedings of the Cambridge Philosophical Society,* Vol. XVII. 1912–14, p. 307, entitled "A possible connexion between abnormal sex limited transmission and sterility," it was suggested that tortoiseshell tom cats are usually sterile. In an earlier paper[1] evidence was given that the rare tortoiseshell male cat might be produced by the failure of the normal sex-limited transmission of the yellow factor from the male parent. When a yellow (orange) male cat is mated with a black female, the normal result is that all the female offspring are tortoiseshell, all the males black, showing that the yellow factor is sex-limited in its transmission by the male, and goes only into the gametes which will give rise to females. There is some evidence, however, which seems to point to the conclusion that tortoiseshell males may be produced by a yellow male parent mated to a black female; this is apparently brought about by the failure of the yellow factor always to pass to female producing gametes. A male produced in this manner would presumably be a tortoiseshell. A tortoiseshell male has been in our possession for more than two years and we have repeatedly endeavoured to mate him with a black female in order to find out how the yellow and black factors are transmitted by a male cat in which both are present. Although copulation has occurred many times with each of four females when on heat, apparently with success, yet pregnancy has never followed with any of the females used. These

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[1] *Journ. of Genetics*, Vol. III. 1913, p. 11.

females all had kittens, before or afterwards, to other sires, so that it seemed evident that the tortoiseshell tom was sterile.

The external genitalia of the cat are perfectly normal: there is a normal well developed penis, and both testes are descended into the scrotal sac; this latter point is important, for as will be shown later failure of descent of the testes is almost invariably associated with sterility.

In order therefore to endeavour to discover the reason of this sterility, in March 1915 we decided to examine one of the testes microscopically in the hope of finding whether at some stage of spermatogenesis an abnormal division took place which prevented the further development of the sperms, as is the case with some hybrids.

Dr F. H. A. Marshall, to whose help we are greatly indebted, undertook the removal of one testis. This seemed perfectly normal, the only difference being that when the testis was cut up preparatory to placing it in preservative, no seminal fluid was exuded, as is usually the case with the normal animal. Different portions of the organ were preserved in strong Flemming, acetic sublimate, and Bonin's fluid, the last giving by far the best results. . Sections of 5μ thickness were cut, and then stained with iron haematoxylin. Upon examination it was found that there was no trace of spermatogenesis, but there was a considerable excess of interstitial tissue between the tubules.

Before describing this in detail, perhaps it would be advisable to give an account of the testis of a normal cat for the sake of comparison.

The tubules are large and placed in fairly close proximity, the spaces between them being filled with interstitial tissue. The individual cells of this tissue are not easy to distinguish one from another, but the nuclei are very distinct and numerous: also it is easy to distinguish what appear to be two types of nuclei, one, which under a low power appears almost black (Pl. XX, Fig. 1, *d.n.*) when stained with iron haematoxylin; the other much lighter showing a distinct nucleolus (Fig. 1, *c.n.*). Examination under a high power reveals the fact that the two kinds of nuclei differ only in that one is more granular than the other: both have the same kind of nucleolus.

Scattered among the cytoplasm there are numerous black granules, which Bonin and Ancel in a paper published in the *Archives de Zoologie expérimentale et générale* for 1903, 4 Série, Tome 1, p. 437, entitled "Recherches sur les cellules interstitielles du testicule de Mammifères," assert to be of secretory origin, and of a fatty nature (Fig. 1, *d.g.*). Vacuolation can also be noted to a small extent. The tubules are

numerous and form the greater part of the whole organ; the cells in them may be arranged in layers according to the condition of the various cells in the development of the sperm. The lowest layer, that nearest the wall of the tubule, is composed of spermatogonia among which lie the Sertoli cells; these are characterised by their lightly stained cytoplasm, their irregularly shaped nuclei, and the presence of a distinct nucleolus; in the human testicle a rod has been described as present in each of these Sertoli cells, but in the cat we have been unable to detect it with any degree of certainty.

The next layer of cells are spermatocytes for the most part and in them can be seen the mitotic figures in various stages of division; while the centre of the tubule is almost entirely filled with mature sperms.

Testes of Tortoiseshell Cat.

As already mentioned the most conspicuous differences between the testes of the normal and tortoiseshell tom cat are the abundance in the latter of interstitial tissue and the entire absence of the spermatogenesis within the tubules (Fig. 2). Turning now to detail, of which a high power drawing is given in Fig. 3, we see that the interstitial tissue is similar in nature to that of the normal cat, the two types of nuclei, *d.n.*, *c.n.* already mentioned, can be easily detected, though the dark type is less abundant than the light; there are also the same darkly stained bodies scattered throughout the cytoplasm which were to be found in the normal male cat (*d g.*). The cells are more vacuolated than in the normal testis, but otherwise the interstitial tissue hardly differs from that of the normal testis except for its much greater amount.

The tubules are smaller than those of the normal cat, and there is always a distinct lumen in the centre. The cells round the periphery resemble Sertoli cells but there is no trace of normal spermatogonia nor of mitotic figures. The Sertoli cells are found in a small amount of protoplasm which is possibly the remains of the degenerated spermatogonia; this protoplasm is vacuolated and strands pass from it into the centre of the tubules.

A section of the epididymis also demonstrates that although this part of the generative system is normal in structure, yet the centre of the tubes are entirely devoid of spermatozoa, while in the normal case the lumen is practically full of them.

The abundance of interstitial tissue is also of interest in connexion with the supposed function of this mass of cells. Bouin and Ancel in the paper quoted above (p. 514) write in regard to the function : " Nous admettons donc que, chez les Mammifères, l'instinct sexuel et les caractères sexuels secondaires (cette expression étant prise dans son sens le plus large) se trouvent sous la dépendance de la glande interstitielle du testicule." This statement has also been confirmed by many authors. In view of this it is worthy of note that in the tortoiseshell male cat investigated, the sexual instincts were exceptionally strongly developed.

Other cases of a similar character.

Owing to the kindness of Dr F. H. A. Marshall we were able to examine sections of the testes of an hermaphrodite pig which was sent to him for examination. A full report of the case can be found in a paper by J. Hammond in the *Journal of Anatomy and Physiology*, Vol. XLVI. 1911–12, p. 307.

Only the reproductive organs were sent for examination, but it was afterwards discovered that the testes were undescended. The male organs were the same on both sides and consisted of testes apparently normal, epididymis, and vas deferens which ran into a seminal vesicle, and which communicated with the urethra in the usual way. The female organs were also found on both sides and consisted of bodies presumed to be ovaries, situated just below the testes, but which microscopic evidence showed to be masses of lymphatic tissue, and of Fallopian tubes which ended blindly by the sides of the testes but were connected at the lower ends with the superior ends of the cornua of the uterus, which was well developed and normal.

The external genitalia were composed of a small penis 2 cm. long, with a small external opening placed on the dorsal side.

Owing to differences in preservation and staining some of the details are not so clear as in the section of the cat, but it is evident (Fig. 4) that the interstitial tissue was essentially of the same nature as that already figured. Some of the individual cells are more definite than in the previous case, but the nuclei are typical. There are, however, very few of the darkly stained granules lying in the cytoplasm, which were so characteristic a feature of both the normal cat and the tortoiseshell cat.

The tubules are smaller than normal and show much vacuolation, but there is no definite lumen. Many cells are situated on the periphery,

which appear similar to those found in the same situation in the other cases mentioned. Owing, however, to the fixation not being quite perfect some of them have shrunk and the well-developed nucleolus which is so characteristic an element of these cells in other cases, is often replaced by granules lying in the nucleoplasm. The few nuclei which have a definite nucleolus have few granules in them and show that they are comparable to the Sertoli cells already described.

Our next examples of this class of organ are those of retained testes in man and the dog. For these we are indebted to Mr W. McAdam Eccles, F.R.C.S., who kindly lent us a number of slides.

A section of a retained testis in the dog of an unknown age, again showed no trace of spermatogenesis. The interstitial tissue was somewhat excessive in amount, but much less than in the tortoiseshell cat. The tubules were small with thickened walls and were filled with vacuolated strands of protoplasm; in these at the margin were a large number of nuclei.

Sections of the retained testis in man vary considerably in different cases, but some show very nearly the same set of characters already mentioned above with one or two differences of a minor nature. The interstitial cells are similar, showing the same characteristic nuclei and vacuolation (Fig. 5), but are less in quantity than in the tortoiseshell cat, and sometimes mingled with a considerable amount of fibrous tissue. In the tubules there is a well-developed lumen, the protoplasm is scant and drawn out into strands radiating into the middle, the nuclei of the cells being placed round the periphery. A frequent feature is the thickening of the walls of the tubules; this is referred to by G. Bellingham Smith (*Guy's Hospital Reports*, LIII. 1896) as a characteristic feature of the retained testis in man, but is not present in the cat or other animals examined by us.

According to a paper by Griffiths in the *Journal of Anatomy and Physiology*, Vol. XXVIII. 1894, p. 209, the man with retained testes has all the sexual instincts; this is in agreement with what we find in the tortoiseshell cat, and as already stated, is in accordance with the hypothesis that the stimulus of the sexual instincts arises in the interstitial tissue.

Attention must now be drawn to the figure and description in the paper by Bouin and Ancel (p. 499), of the testis of a guinea-pig examined 78 days after the ligature of the vas deferens. They say: "Les spermatozoïdes disparaissent tout d'abord, puis les spermatides, les

spermatocytes et enfin les spermatogonies. Chez un animal sacrifié cent deux jours après le ligature de deux canaux déférents, les tubes testiculaires sont très reduits de diamètre; ils renferment seulement quelques noyaux de Sertoli semés dans un protoplasme indivis.…Les cellules interstitielles subsistent entre les tubes séminifères. Elles forment, comme dans le testicule normal, des cordons et des traînées situés dans les carrefours glandulaires. Elles renferment dans leur cytoplasme des granulations acidophiles et quelques globules de graisse. Le testicule que nous avons ainsi transformé expérimentalement ressemble donc tout à fait au testicule d'un animal cryptorchide."

Finally in the same paper by Griffiths as that quoted above, p. 218, it is shown that when a normal testicle is replaced in the abdomen, all care being taken not to injure the organ and to re-establish vascular connexion, it dwindles in size and becomes like a young one which has not developed, there being no trace of spermatogenesis.

From the facts here described, it is clear that the testis of our tortoiseshell cat resembles rather closely the testis in which sterility is associated with retention within the abdomen. Incidentally, therefore, it throws light on the problem which has given rise to some dispute, as to whether the abnormality of the retained testis is a cause or a consequence of its retention. Some maintain that the testis fails to descend because it is abnormal; others that the abnormality is due to the failure to descend into the scrotum. The evidence collected by Bellingham Smith in the paper mentioned above, coupled with the results of transplantation experiments, seems to us to point clearly to the conclusion that sterility is a consequence of retention, and this is confirmed by the condition found in the tortoiseshell cat, in which the testes were normal in position although totally sterile. The sterility in this case is clearly due to some other cause, and the question arises whether it is connected with the possession by the animal of a colour found normally only in the female. If so, then other tortoise-shell tom cats should also be sterile, as was suggested in the note referred to at the outset of this paper. We have found that evidence bearing on the question is somewhat difficult to obtain. Mr E. T. Cox, secretary to the "Governing Council of the Cat Fancy," has kindly examined the registers in his keeping, and finds no single case in which a tortoiseshell or tortoiseshell-and-white (tricolour) tom is recorded as a sire. This, though purely negative, is in itself evidence that tortoiseshell toms are not usually fertile, for, although they are un-doubtedly rare, for this very reason they are prized by cat-fanciers, who

generally hope that by mating male and female tortoiseshells together they may be able to breed tortoiseshell male kittens. More positive, but not very conclusive, evidence is supplied by Sir Claud Alexander, Bart., who has probably had more experience of tortoiseshell (or "tricolour") toms than any other person. He has at different times possessed five, and has probably seen the few others that have been shown at the more important shows in recent years. One only of these, "Samson," was undoubtedly fertile; he sired many kittens by tortoiseshell dams, but produced no tortoiseshell males. Of the remaining four, one died before he was mated; the second, which appeared quite normal, "mated freely but got no kittens." The third "had a long life, served many 'queens,' and got no kittens," but in one case a female after being served by him was sent away and not kept under strict observation, and produced one weakly kitten which soon died; it is possible therefore, but not certain, that this cat was not totally sterile. The fourth cat was old when he came into Sir C. Alexander's possession, and so savage with females that he was never successfully mated. His previous owner, however, was confident that he had sired kittens in his youth, but there is no direct evidence that the females served were kept rigidly separated from other males. Finally, in the case of the famous tortoiseshell tom "King Saul" which belonged to the late Mrs Herring, Sir Claud Alexander writes that he was believed to have sired kittens, but there appears to be no certainty of this, and no such kittens appear to have been registered[1].

Altogether, therefore, it appears that of six tortoiseshell or "tricolour" toms about which some information is available, one was quite fertile, two completely sterile, and one other almost if not totally sterile: the remaining two are doubtful; they are reputed to have become parents, but the evidence is not conclusive. From these facts it is clear that tortoiseshell toms may at least sometimes be fertile, but that a considerable, and possibly large proportion of them are sterile. The question arises whether the sterility is in some way a consequence of their possessing the colour-factors normally found only in the female, or whether the sterility is the primary feature, which leads to the development of colour proper to the female. It is impossible to give a final decision, but on the whole, the evidence points to the conclusion that the sterility is a consequence of an abnormal hereditary constitution. It is clear that, since the cat "Samson" was fertile, his

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[1] Miss F. E. Frowd has kindly searched old catalogues and made enquiries, without succeeding in tracing any progeny of "King Saul."

colour cannot have been due to sterility, whereas it is not impossible that the abnormal transmission of a sex-limited colour-factor to a male may sometimes cause the animal to be sterile, and in other cases not have this effect, just as retention of the testes in the abdomen does not always lead to total sterility. In this connexion it is interesting that similar phenomena are said to be found in breeds of fowls, such as the Sebright, in which the male may be hen-feathered. It is supposed by some fanciers that in these breeds completely hen-feathered cocks are not infrequently sterile, and in consequence cocks which are only partially hen-feathered are generally used for breeding. Prof. Punnett has kindly given us sections of a testis of a completely hen-feathered cock, extracted from the cross Sebright hen × Hamburgh cock, in which the tubules contain no trace of spermatogenesis, but are in general similar to those of the tortoiseshell tom cat (Fig. 6). They differ chiefly in being lined with many cells with rather small nuclei, instead of the comparatively few large cells—which we have compared with Sertoli cells—found in the cat. There is also a somewhat increased amount of interstitial tissue, a fact which would be of considerable interest in a cock with the female type of plumage if it were certain that the interstitial tissue of birds had a secretory function like that of Mammals. The interstitial tissue of the normal fowl is smaller in amount than in the mammals, and it is maintained by Miss A. M. Boring (*Biol. Bull.* XXIII. 1912, p. 141) that it consists simply of connective tissue, and has no secretory function. The testis of the hen-feathered cock supports her conclusion to this extent, that the interstitial cells contain neither the vacuoles nor the secretory granules which are so conspicuous in the cat (Fig. 6, *i.t.*). The tissue is, however, not by any means entirely fibrous, but seems to consist of cells with fibres running among them and it is doubtful whether it can properly be described as connective tissue. In any case, the testis of the hen-feathered cock supports the conclusion that the sterility is a consequence of the possession of an abnormal hereditary factor, for hen-feathering is undoubtedly due to such an inherited factor, and is not a mere consequence of sterility, so that the cases of the tortoiseshell cat and hen-feathered cock taken together suggest that when a male animal receives a factor, either normally or through failure of the normal sex-limited transmission, which causes it to assume characters proper to the female, there is a tendency for sterility to appear.
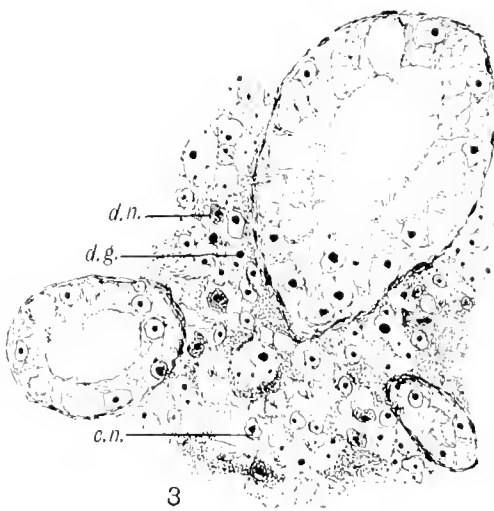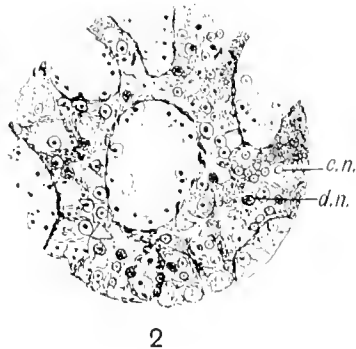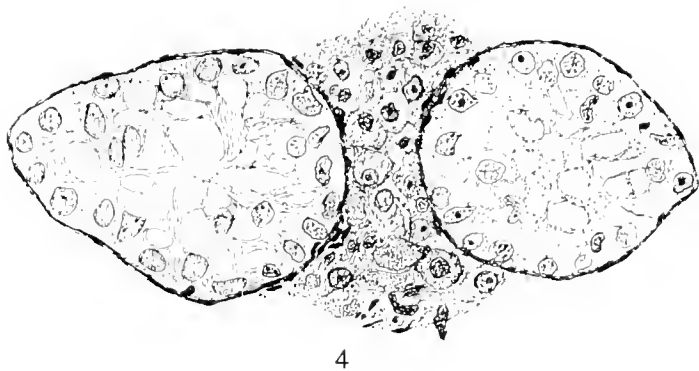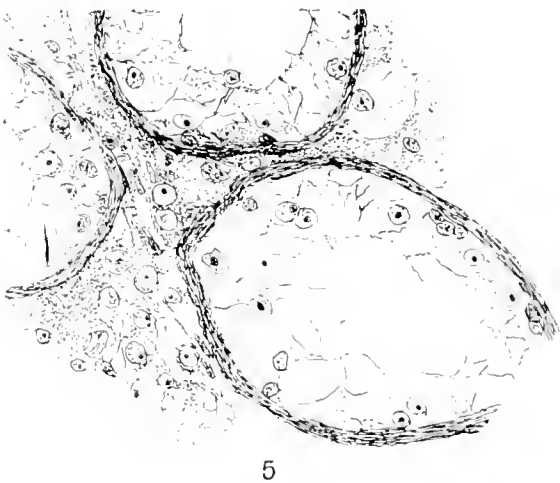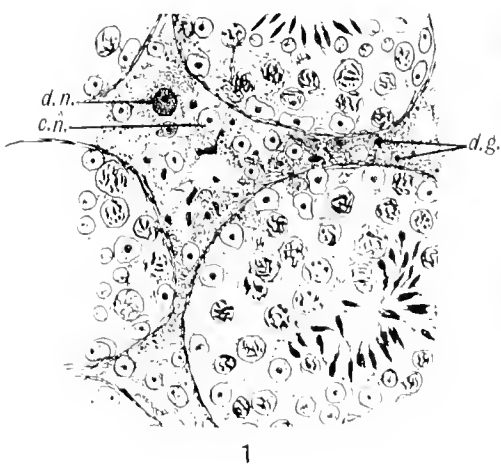
EXPLANATION OF PLATE XX.

Fig. 1. Portion of testis of normal cat (2 mm. immersion lens). The amount of interstitial tissue represented is rather unusually large ; *c.n.* light nuclei of interstitial tissue ; *d.n.* darkly-stained nuclei of interstitial tissue ; *d.g.* secretory granules.

Fig. 2. Portion of testis of tortoiseshell tom cat, low power.

Fig. 3. Similar portion drawn with 2 mm. immersion lens. Lettering as in Fig. 1.

Fig. 4. Portion of testis of hermaphrodite pig (2 mm. immersion lens).

Fig. 5. Portion of human retained testis, showing the thickened walls of the tubules, but otherwise similar to the preceding specimens. The fibrous structure of the interstitial tissue found in some cases, is not seen in this specimen. 2 mm. immersion.

Fig. 6. Portion of testis of hen-feathered cock. 2 mm. immersion. *i.t.* interstitial tissue.

"GYNANDROMORPHISM" AND KINDRED PROBLEMS.

WITH DESCRIPTIONS AND FIGURES OF SOME HITHERTO UNDESCRIBED EXAMPLES.

By E. A. COCKAYNE, M.D., M.R.C.P., F.E.S.

CONTENTS.

OCCURRENCE OF GYNANDROMORPHISM.

Structure and Classification.

SEXUAL dimorphism is so well marked in insects, especially in the Lepidoptera, that the two sexes of the same species have sometimes been assigned to different species and even to different genera. Very striking therefore is the appearance of those individuals which show on one side all the characters, size, shape, and colour of the one sex, and on the other, those of the opposite sex. Their existence was known

long before any dissections were carried out and the term gynandromorphous or gynandrous was applied to them. The first dissection was carried out in 1825 by Rudolphi on a halved gynandromorphous *Gastropacha quercifolia.*

Later it was recognised that, besides the halved, other forms of gynandromorphism also occur and in this country Westwood drew special attention to these and figured several in his *Thesaurus Entomologicus Oxoniensis.* The term means no more than the occurrence in one sex of characters belonging to the other, and covers more than one very distinct phenomenon.

It is much better known and probably much commoner in insects than in other animals. But of other Arthropods, Bertkau gives examples in various crustaceans and two in Arachnida, both in spiders.

His list includes instances in all the better known orders of the Insecta, in Lepidoptera, Hymenoptera, Coleoptera, Diptera, and Orthoptera. There is little doubt that it is much more frequent in some of these orders than in others, but so much less attention is paid to some and the phenomenon itself is so much less conspicuous in some than in others, that no very exact deduction as to the relative frequency can be drawn. Several thousands have been recorded in Lepidoptera, but in Hymenoptera, which are also carefully worked, Dalle Torre and Friese could only collect 90 examples, though they left out those produced in the Eugster hive of bees, which alone numbered some hundreds.

In Lepidoptera it is unquestionably much commoner in some species than in others, as the lists published by Hagen, Wiskott, and Schultz prove.

The difference in numbers is real and not apparent, because in *Amorpha populi,* which heads the list, gynandromorphism is not so conspicuous as in many equally common species, of which only one or two gynandromorphous individuals are known.

Schultz in his first two lists of gynandromorphs in Palaeartic Lepidoptera gives *A. populi* 54 examples, *Saturnia carpini* 48, *Dryas paphia* 39, *Lymantria dispar* 32, and *Polyommatus icarus* 22.

Five examples are known in birds.

Four of these were perfectly halved, a bullfinch, *Pyrrhula pyrrhula europaea,* Vieill, described and figured by Heinroth and Poll, a chaffinch, *Fringilla coelebs,* Linn., described by Weber, a flicker, *Colaptes auratus,* Linn., and a species of *Dacnis,* a South American sugar bird. The fifth, a pheasant described and figured by Bond, was perfectly halved, except in the tail, and there was some decussation of sex characters, each feather of both sides being male on the outer and female on the inner side.

In man Garrigues stated, in 1896, that he knew an individual, who on the left side looked like a male, on the right like a female. Partial segregation of secondary sexual characters to opposite halves of the body, has also been recorded by Munde, Oberndorf, and Le Dentre.

Lists of gynandromorphous Arthropods have been published by Hagen, Ochsenheimer, Bertkau, Wiskott, and Schultz.

Ochsenheimer divided them into perfect and imperfect, and Lacordaire further subdivided them into—

(1) Semilatéral (halved).

(2) Superposé (intermediate mixed forms).

(3) Croisé (crossed).

In addition he pointed out that in all three forms the sexual elements may be in equilibrium, but in the last two one or other sex may predominate to any extent.

A very elaborate classification has been made by Dalle Torre and Friese.

Group I. Lateral Gynandromorphism.

1. Left ♂, right ♀. (a) Head alone.
2. Right ♂, left ♀. (b) Thorax alone.
3. Decussating now ♂ right. (c) Abdomen alone.
        now ♂ left. (d) Head and thorax.
            (e) Head and abdomen.
            (f) Thorax and abdomen.
            (g) Whole body.

Group II. Transverse Gynandromorphism.
(Dorso-ventral arrangement.)

1. Dorsally ♂, ventrally ♀. Subdivisions (a) to (g) as
2. Dorsally ♀, ventrally ♂. in Group I.

Group III. Frontal Gynandromorphism.
(Antero-posterior arrangement.)

1. Anteriorly ♂. (a) Head alone.
2. Anteriorly ♀. (b) Head and thorax.
            (c) Thorax of one, head and abdomen of the other sex.

Group IV.   Mixed Gynandromorphism.

(Lateral, transversal and frontal intermixed.)

1.   Left   ♂.   5.   Dorsally ♂.
2.   Left   ♀.   6.   Dorsally ♀.
3.   Anteriorly ♂.   7.   Decussating.
4.   Anteriorly ♀.

Nearly all gynandromorphs fall into the fourth group.

The dorso-ventral arrangement of the external characters has been met with once, and the antero-posterior rather more frequently. I have seen two specimens of *Saturnia carpini* with a male head and antennae, the rest of the insect being female, and Mr Bright has a similar example of *Orgyia antiqua* ; Schultz records a *Demas coryli* with female head and antennae and a male thorax and abdomen. Lateral gynandromorphism of the external characters, excluding the genitalia, is common. But in a very large number of instances the halving is not quite perfect.

From those insects which show an almost complete halving of external characters we pass gradually to those which show a very coarse mosaic arrangement, the male element preponderating on one side and the female on the other, and thence to those where the two elements are almost evenly balanced.

In others the coarse mosaic is met with, but one or other sex greatly preponderates. In others again the mosaic is found finer.

A fine mosaic arrangement, where there is a very intimate bilateral mixture, gives the "gynandromorphe superposé," such as the *Polyommatus icarus* figured later (Pl. XXIV, fig. 19).

The upper side of this is predominantly male, but amongst the small patches with blue scales and androconia, less numerous patches of brown scales of female shape occur. Orange scales representing female lunules also occur on the margins. The underside is predominantly female. Wheeler has described "blended gynandromorphs" with the form of one sex, the colours, sculpture or pilosity of the other. In these I believe the mosaic arrangement still holds good, but that cells of male and female type are arranged much as the cells in a plant chimaera (graft hybrid).

In these the core, which gives the form, is made purely of cells of the one species and the external layer or layers of cells made purely of those of the other species. Cells of intermediate character do not occur in these plants, nor do they, I think, occur in such gynandromorphs,

though there may be a rather intimate mixture of cells of male or female character.

The more gynandromorphs one sees the more unsatisfactory does any attempt at classification by external characters appear to be.

Unfortunately classification based on internal structure is greatly hampered by the small number of dissections carried out and described. This is partly due to the difficulty of dissection, but far more to the value of these specimens, and the reluctance of their owners to allow any examination. The following classification is based on the somewhat less elaborate one suggested in the *Entomologist's Record*.

I. Genetic Hermaphrodites.

Primary sex glands of both sexes present.

I. *Lateral.*

   (*a*) Ovary on one side.
         Testis on the other.

   (*b*) Two ovaries on one side.
         Testis on the other.

   (*c*) One ovary on one side.
         Two testes on the other.

   (*d*) Two ovaries on one side.
         Two testes on the other.

II. *Unilateral.*

         Ovary *or* testis on one side.
         Ovary *and* testis on the other.

III. *Bilateral.*

         Ovary and testis on both sides.

II. Primary Somatic Hermaphrodites.

Sex gland or glands of one sex only, but parts of the secondary sexual apparatus, internal or external, of both sexes present.

   (*a*) Male type, with one testis or two testes.

   (*b*) Female type, with one ovary or two ovaries.

In some cases the glands are perfectly developed, but a partial or completely rudimentary condition is not uncommon, especially in the ovary.

III.   Secondary Somatic Hermaphrodites.

Sex gland or glands of one sex only; secondary sexual apparatus of one sex only, that corresponding to the sex gland present. Secondary sexual characters of both sexes present in antennae, wings, or other parts of body.

(*a*)   Male type, with one or two testes.

(*b*)   Female type, with one or two ovaries.

The majority of gynandromorphous insects fall into Group II, primary somatic hermaphrodites, relatively few into Groups I and III.

Of genetic hermaphrodites the only examples which can be included in the bilateral group are the *Lymantrias* bred by Goldschmidt and others, which had ovarian and testicular tissue mingled in the follicles of both gonads (Zwitter-drüse).

In the unilateral group is a specimen of *Polyergus rufescens* Latr. described by Wheeler and an *Amorpha populi* figured by Wenke.   The latter had two ovaries, one very rudimentary; but their oviducts opened into vesiculae seminales, and below this the ducts each gave rise to a glandula accessoria and then ended blindly.   Attached to the side of one ovary there was a testis containing no spermatozoa.   To explain the existence of genital organs arranged in this mosaic manner, we must suppose that a mosaic arrangement of cells occurred in the germinal epithelium and primitive genital tract.   The germinal epithelium of one side must have consisted of cells wholly female in character and so gave rise to an ovary; that of the other side must have been divided longitudinally into a part consisting of cells of female character and a part consisting of cells of male character.   The former gave rise to a rudimentary ovary and the latter to a rudimentary testis.

An irregular mosaic arrangement of the embryonic tissue of the lower part of the genital tract gave rise to the irregular mosaic arrangement of male and female sexual organs.

Such a mosaic arrangement of embryonic tissue giving rise to the wings and other parts of the body almost certainly occurs, and there seems to be no reason why a similar arrangement should not occasionally occur in that from which the gonads and other parts of the sexual apparatus arise.

The great majority of genetic hermaphrodites in insects fall into the lateral group.   The gynandromorphous birds are also lateral genetic hermaphrodites and are all alike in having a testis on the male side and an ovary on the female.

In the lobster, *Homarus vulgaris*, described by Nicholls before the Royal Society in 1730, this condition was also present.

There was perfect halving in all respects both external and internal.

Though perfect halving of external parts is common in insects, it is very rarely met with in the genital apparatus. In Lepidoptera only a single instance is on record, that described by Toyama in *Bombyx mori*. But we cannot suppose that there is any fundamental difference between the halved gynandromorphous insects and birds. The most simple explanation of the very varied appearance met with in the sexual apparatus in halved gynandromorphous insects is that there is a tendency for the halves of the germinal epithelium and primitive genital tract each to form a complete sexual apparatus, including two gonads, by completion of unpaired median organs and doubling of paired lateral organs.

Sometimes the doubling does not affect the gonad, but only the accessory glands or ducts or the external genitalia.

Associated with this there is often a failure in development of part of the sexual apparatus of both sides.

Examples of this are the *Melitaea didyma* and the *Saturnia spini* figured by Wenke, each with two testes on one side and two ovaries on the other, with many of their respective accessory organs. In both cases the glandulae accessoriae failed to develop.

Examples where the doubling has only affected the lower part of the genital tract are two of the three specimens of *Amorpha populi* figured and described later (Nos. 6 and 8, Diagrams *f* and *h*).

Sometimes one half shows a tendency to develop perfectly, with or without doubling, whilst the other half fails to develop in its lower part. An example of this is afforded by the *A. populi* figured and described later (No. 7, Diagram *g*).

If the upper part of the tract, which forms the gonad, fails to develop on the one side, as it does very frequently, a primary somatic hermaphrodite is produced. The other half may produce a single set or a double set of sex organs, and the doubling may affect the gonad. Examples of this condition with doubling of the testis are specimens of *A. populi*, such as the one I figure later; with doubling of the ovary, an *A. populi* and a *Vanessa antiopa* figured by Wenke, and with a single ovary, a *Dryas paphia* also figured by Wenke, Gerstäcker's *A. populi*, and an ant, *Leptothorax tuberum*, described by Wheeler.

On the side, which has failed to develop its gonad, all the other sexual organs may be present, or only the lowest part of the internal

genital tract or a part of the external genitalia may be found, but the part which is found may show doubling.

There is thus no fundamental difference between lateral genetic and many primary somatic hermaphrodites.

Secondary somatic hermaphrodites are probably quite different, and one point which supports this is that two gonads have been present in all the cases investigated.

Examples of Secondary Somatic Hermaphrodites of male type appear to be rare. One is figured by Wenke and described by O. Schultz. It is a *Lymantria* (*Ocneria*), externally male in shape and colour, but with streaks of female colour on both forewings.

The *L. dispar* similar in external appearance, bred by Schütze and described later, were probably similar internally also, since two of them proved fertile when paired with normal females.

The only undoubted examples of female type are the six *Agriades coridon* dissected by me and described fully in the *Entomologist's Record*, but all the similar gynandromorphs from the same locality are probably of the same constitution. The *Agriades coridon* females streaked with male colour dissected by Dr Chapman and myself, may belong to this group, but their exact nature is still uncertain[1].

Gynandromorphism associated with Heterochroism.

A considerable number of instances are now known in which an insect, in addition to being gynandromorphous, exhibits the colour and pattern of the type form in all the parts which are of one sex, and those of some varietal or aberrational form in all the parts which are of the other sex.

The dimorphism is not sexual; for both the type form and the aberrational form occur equally in normal males and females of the species in a majority of these cases. Further than this these strange

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[1] Since this paper has been in the press Duncan has published an interesting note on the gonads of *Drosophila ampelophila* in the *American Naturalist*, 1915, Vol. XLIX. p. 455. Five specimens were dissected one of which was perfectly halved, the others showing some crossing of secondary sexual characters. So far as the examination went all showed halving of the genital armature. The gonads were in three cases male on both sides, in two female on both sides. None had any sexual instinct though four were courted in vain by one or more males.

The perfectly halved specimen was heterochroic, being red-eyed on the female side and white-eyed (a sex-limited character inherited in the same way as colour-blindness in man) on the other. Another specimen also showed heterochroism, being red-eyed on one side and cherry-eyed on the other.

gynandromorphs not only exist in the halved and nearly halved forms, but also in the crossed and coarse mosaic forms. For this segregation of distinct colours and patterns, which are quite unconnected with sex, I use the term heterochroism.

Examples recorded in Schultz's lists, which merely record palaearctic gynandromorphs, with additions from recent literature and a few hitherto unrecorded examples are appended below.

(1) *Aglia tau* and ab. *lugens* (*nigerrima*).

Several of these are known : in some the male portions were type form and the female ab. *lugens*, in others the reverse occurred. They were completely halved or crossed, and in one a single hindwing showed female shape with the colouring of ab. *lugens*.

The antennae were intermediate between the male and female in the ones showing a coarse mosaic. Gynandromorphs with both sides typical or both melanic are known.

(2) *Psilura monacha*.

(*a*) Upper side of left forewing female with type colouring, the rest, including both antennae, and the abdomen male, with the black colour of the aberration *eremita*.

(*b*) Halved; left side female type colour, right side male ab. *eremita* except for a small patch in hindwing.

(*c*) Halved : left side male typical, right side female *eremita*, the division extending down the centre of the thorax and abdomen.

In this species also halved gynandromorphs wholly typical and wholly ab. *eremita* are known.

(3) *Hemerophila* (*Synopsia*) *abruptaria*. (Previously unrecorded.)

(*a*) Halved : left side female type (buff colour), right side male ab. *brunneata* Tutt (chocolate colour). Abdomen thin and wholly typical. External genitalia of (?) both sexes. (Pl. XXI, fig. 1.)

(*b*) Left side female type except for a melanic area on hindwing on upper side, and another on forewing on under side : right side ab. *brunneata*. Abdomen thin.

(*c*) Left side male type, right side female ab. *brunneata*. Abdomen stout, half melanic, half typical.

(*d*) Left side female type, right side male ab. *brunneata*.

Gynandromorphs are known with both halves typical.

(4) **Acidalia virgularia.**

Left side male ab. *bischoffaria* (melanic), right side female type. This was bred by Habich, the other imagines of the brood were type and ab. *bischoffaria*.

(5) **Amphidasys betularia.** Halved.

Right side male ab. *doubledayaria* (melanic), and left side female ab. *mixtus*. (Intermediate.)

(6) **Angerona prunaria.** Halved.

Right side male, left side female. One side var. *sordiata*, the other typical.

Halved gynandromorphs with both sides *sordiata* and both typical are known.

(7) **Abraxas sylvata.** (Previously undescribed.) Halved.

Left side female type, right side male ab. *pantarioides* (Pl. XXI, fig. 2). Bred from larva found at Limber, Lincolnshire, 1899.

(8) **Ematurga atomaria.** (Previously undescribed.)

Mosaic, left antenna half pectinated, half simple, right antenna simple. All the wings show a coarse mosaic of male melanic colour, and female typical speckled grey colour. It was bred in 1910 by Mr L. W. Newman from Bury larvae, which also produced typical and melanic specimens, and is in Mr P. M. Bright's collection.

(9) **Lithosia aurita.** Halved.

Left side male type *aurita*, right with female ab. *ramosa* Fabr.

(10) **Phragmatobia sordida** Hb. Halved.

Left side female ab. *trifasciata* Mill, right side male ab. *carbonis* Fr. Hyckel, *Ent. Zeitschr.* XVIII, p. 56.

(11) **Bombyx trifolii.** Halved.

Left side male, var. *medicaginis*, right side female type.

(12) **Anthrocera trifolii.** Halved.

Right side male, var. *orobi*, left female, var. *confluens.*

(13) **Dicycla oo.**

(*a*) Right side male typical, left female ab. *renago.*

(*b*) Right side male type, left female ab. *renago.*

(14) **Amorpha populi.**

(*a*) Right side male ab. *rufescens*, left side female type.

(b) Right side male type (grey), left side female *?* ab. *rufescens* (deep pink), right antenna showed slight male characters, left wholly female.

(c) Right side female *?* ab. *rufescens* (deep pink), left side male type (dove grey).

Many *A. populi* gynandromorphs show great difference in ground colour on the two sides, which is not a sexual one. Sometimes the male side is red-brown, and the female grey; sometimes the reverse is the case.

(15) *Erebia pronoe* Esp. Halved.

Right side male var. *pitho* Hb., left side female type.

(16) *Apatura ilia* Schiff.

(a) Right side male *ilia* type, left side female ab. *clytie* (one example).

(b—d) Right side male ab. *clytie*, left side female *ilia* type (three examples).

(e—g) Left side male *ilia* type, right side female ab. *clytie* (three examples).

(h) Left side male ab. *clytie*, right side female *ilia* (one example).

These eight are all halved.

(i) Left side male predominant, and where most clearly male in shape and size it was coloured with ab. *clytie*; rest wholly female, *ilia* type.

(17) *Ganoris rapae* ab. *flavescens*.

Left side female ab. *flavescens* (yellowish brown).

Right side male and white in colour, with streak of yellow female colour (ab. *flavescens*). *Soc. Ent. Zurich*, XVIII, No. 10, p. 80.

(18) *Limenitis populi*.

(a) Right side male ab. *tremulae* Esp., left side female type.

(b) Right side male ab. *tremulae* Esp., left side female type.

(c) Right side male ab. *tremulae*, left side female type.

(19) *Araschnia levana*.

Right forewing small male and var. *prorsa* L.: right hindwing and both wings on left side large and ab. *porima* Ochs.

(20) *Aricia eumedon*.

Left side female type, right side male ab. *fylgia* Spangb.

(21)   *Hybernia leucophaearia.*

Right side ab. *marmorinaria* Esp., left side wingless type female.

It is noteworthy that some of these forms have been proved to be Mendelian dominants to the others. The melanic form of *H. abruptaria*, for instance, is dominant to the type, as are *A. virgularia* ab. *bischoffaria*, *A. prunaria* var. *sordiata*, the melanic form of *E. atomaria*, and **Aglia** *tau* ab. *lugens*, though in this last case, according to Sturtevant, there is a partial sex linkage of the character for ab. *lugens* with that for the male sex.

The intermediate form of *A. betularia* is probably an imperfect dominant, the black form ab. *doubledayaria* × type usually produces half ab. *doubledayaria*, half type, when the black parent is heterozygous. *Doubledayaria* × *doubledayaria* may give all *doubledayaria*. Intermediates are rare.

In the case of the four gynandromorphous *H. abruptaria*, they were the result of a pairing between a heterozygous dominant and a homozygous recessive, and this was probably the case in some other instances.

Larvae which showed Heterochroism and produced Gynandromorphous imagines.

These occurred in the silk-worm (*Bombyx mori*). Toyama records two larvae completely halved with the left side zebra banded and the right unicolorous white.

They were bred from a male of Japanese unicolorous strain and a female of European zebra strain. One produced an imago which was a gynandromorph completely halved in all respects, right side male, left side female.

Mayer in the *Ent. Zeitschr. Stutt.* XXIII, p. 104, records a larva from a cross of an Italian and a French race which was black on the whole of the right side and white on the left side. This produced a gynandromorphous *B. mori* with the right half completely male, and the left half completely female; even the external genitalia, though rather crippled, were completely halved.

Blaringhem (*C. R. Soc. de Biol.* Paris, 1913, 74, p. 1291) describes a larva with the right side wholly unicolorous white, the left side zebra with a mosaic of white patches on the posterior half. It was found amongst 1,200,000 larvae all normal of a strain which was almost entirely zebra, though white specimens occasionally appeared.

He refers to three other larvae which showed a mosaic of white and dark colour, and says the condition is excessively rare but is well known to silk-worm breeders.

Toyama has proved that the zebra is a simple dominant to the unicolorous white.

Insects showing segregation of somatic characters (Heterochroism) but no segregation of sexual characters (Gynandromorphism).

(1) *Acidalia virgularia.*

Right side ab. *bischoffaria*, left side type. Bred by A. Bacot, with specimens wholly melanic (ab. *bischoffaria*) and wholly typical. External characters and external genitalia were of one sex only. The secondary sexual characters in this species, especially in the antennae and legs, show marked dimorphism.

(2) *Abraxas sylvata.*

Tutt in the *Entomologists' Record*, 1897, IX, p. 306, describes the capture of several heterochroic examples of this species.

(*a*) One with left forewing dull smoky grey (ab. *suffusa* Tutt), the other three wings being normal.

(*b*) Others showing various mosaic arrangements of type colour and that of ab. *suffusa*.

(*c*) One with right forewing suffused with smoky cream colour (ab. *obscura* Tutt), the other three wings being typical.

(*d*) One with left forewing ab. *obscura*, the other three wings being typical.

The ab. *obscura* has both forewings of smoky cream colour and both hindwings of the normal white, so that these last two examples may be regarded as half ab. *obscura* and half type.

The ab. *suffusa*, on the contrary, has all four wings of a leaden grey.

These specimens were all taken in the same wood at the same time, in a year when the ab. *obscura* and ab. *suffusa* were both most unusually common.

(3) *Abraxas grossulariata.*

At the Lancashire and Cheshire Entomological Society in November 1914, Mr R Tait, Junr., exhibited a specimen with the wings on the left side black, with the exception of a few white marginal streaks,

ab. *nigra*, and those on the right typical. The thorax and abdomen were equal on the two sides and half black, half typical.

The specimen is a female. By the courtesy of Mr Tait I am enabled to figure it (Pl. XXI, fig. 2). It was bred from a brood of Huddersfield larvae, all the rest of which produced ordinary *grossulariata*.

Mr G. T. Porritt has proved by his careful breeding experiments that the rare ab. *nigra* is the extreme form of the ab. *nigrosparsata*, and like it does not breed on simple Mendelian lines. The ab. *nigra* × ab. *nigrosparsata* produced all typical *grossulariata* in F_1 and again in F_2, as also occurred in a cross of *nigrosparsata* × *nigrosparsata*. Yet another pairing of *nigrosparsata* × *nigrosparsata* produced all *nigrosparsata* in F_1 and all *grossulariata* type in F_2 (*Entom. Monthly Mag.* 1914, p. 65).

(4) *Tephrosia biundularia* (*crepuscularia*).

Barrett in his *British Lepidoptera* states that in Derbyshire and other parts of the Midlands specimens of this insect are found in which the wings are largely of the melanic form ab. *delamerensis*, but with sharply defined areas, often wedge shaped, of the cream colour of the type form. One of these is figured. Eighteen examples were in Mr G. O. Day's collection and were, I believe, bred from one pair. There were no external evidences of gynandromorphism, and they are probably to be regarded as instances of the segregation of a Mendelian dominant character (ab. *delamerensis*) from a recessive (type colour).

(5) *Chelonia caia* L.

(*a*) The left side typical with brown and white forewing, and red hindwing with blue-black spots, the whole of the right forewing unicolorous brown, and the hindwing blackish brown with the metallic spots showing very faintly. This was bred from a Huddersfield larva, and is in Mr Sidney Webb's collection. A figure is given in Mosley's *Varieties of British Lepidoptera*, Chelonia, Plate VI, fig. 3. The wholly dark form is a very rare aberration.

(*b*) Wings, right side typical, left side completely melanic; abdomen normal. This is a female. Standfuss, *Handbuch*, p. 206.

(6) *Arctia villica*.

An exactly halved example with the right side typical, the left albinistic. The left forewing has all the normal black ground colour replaced by creamy yellow, the hindwings are of the normal rich yellow with black spots, but the spots are not symmetrical on the two sides.

The right half of the thorax is black, the left half creamy yellow. This is described by Oskar Schultz, *Ent. Zeitschrift*, 1906–7, XX, p. 26.

(7) *Psilura monacha.*

(*a*) From a pairing of *P. monacha* × *eremita* were bred two males and 20 females of *monacha*, and 18 males and five females of ab. *eremita*.

In addition there were five males and one female showing on their wings a coarse mosaic of *monacha* type colour and the black colour of *eremita*.

One of these is figured in Standfuss' *Handbuch der paläarktischen Gross-Schmetterlinge*, 1896, and described, p. 308.

(*b*) *Psilura monacha* ♀. Left forewing darkish form, right completely black, ab. *eremita*. Left hindwing pale, right bluish. Abdomen left half typical pink, right half black, ab. *eremita*. Stichel, *Zeitschr. f. Wissensch. Insektenb.* 1912, vol. VIII, p. 41, figure and description.

(8) *Aglia tau.*

In 1887 Hartmann bred a female with the whole of the right side, including half the thorax and abdomen, melanic (var. *lugens*) and the left side typical. *Berl. Ent. Zeitschr.* 1888, XXXII, p. 239.

(9) *Spilosoma menthastri.*

A male specimen is figured in the *Entomologist*, 1909, XLII, p. 224. The left half is striated with black (ab. *walkeri* Curtis), the right half shows the usual small black spots of the type. The ab. *walkeri* is a rare one. A somewhat similar specimen was in the Maddison collection, and is figured in Oberthür's *Lep. Comp.*

(10) *Anthrocera trifolii.*

On the same page of this journal, a male example of this burnet is also figured. The left half is the uncommon ab. *minoides* Selys, with all the red spots confluent; the right half is typical. Mr Bright has kindly allowed me to examine it, and it shows no evidence of gynandromorphism. Both valves are large and well-formed.

(11) *Anthrocera trifolii.*

South in discussing the above specimen describes a somewhat similar example.

The right side was typical, but on the left the spots were partly confluent, 1 and 2 being joined, and 3, 4, and 5. This was a female.

(12) *Syntomis phegea* L.

A most interesting specimen is figured, and described in the *Berliner Ent. Zeitschrift*, 1911, pp. 21 and 32. The left forewing is quite black,

ab. *iphimedia* Esp.; the right forewing is typical, black with white spots; both hindwings have a single white spot. It was taken at Klausen, flying with specimens of the type and the completely black ab. *iphimedia*.

(13)   *Theretra porcellus.*

Wings on right side of normal Southern colouration, wings on left side of the unicolorous yellow shade often seen in Northern specimens. *Ent. Record*, XIX, p. 243.

(14)   *Ganoris (Pieris) brassicae.*

The whole of the right side and the greater part of the left is of the smoky ab. *obscurata*, a rare form. There are large areas of typical white colour on the forewing and hindwing on the left side.

The specimen was taken near Paris, where a specimen completely ab. *obscurata* has also been captured. It is figured in Oberthür's *Lépidopt. Comparée*, XX, 1896, Pl. 1, fig. 5.

(15)   *Polyommatus icarus.*

On the underside the spots are normal on the wings of the left side, absent on the right (ab. *obsoleta*). Sabine, *Entomologist*, 1887, XX, p. 288.

(16)   *Agriades coridon.*   (Plate XXII, figs. 11 and 12.)

Right side: ab. *aurantia* Tutt, upperside: ab. *parisiensis* Gerh., underside.

Left side, typical both on upper and underside.

(17)   *Colias edusa.*

(*a*)   A female with the right side typical *edusa* (orange), the left side ab. *helice* (cream coloured). This was shown by Mrs Hemming at the South London Nat. Hist. Soc. 1913.

(*b*)   A female with the right side ab. *helice* and the left side typical *edusa*. *Entomologist*, 1878, p. 49 (coloured plate).

(*c*)   A female with both forewings ab. *helice*, and both hind wings typical *edusa*. *Entomologist*, 1878, p. 49 (coloured plate).

(*d*)   A female with left forewing ab. *helice*, the other three wings *edusa*, of which coloured figure is given in Mosley's *Varieties of British Lepidoptera* (Colias, Plate 2).

(18)   *Colias philodice.*

A female with the left side yellow and the right side white was captured by J. H. Rogers at Medford, Mass. and is figured in *Psyche*,

1904, XI, Plate X, fig. 4. The right side is much smaller than the left and the costa of the right forewing is abnormally curved.

A phenomenon exactly comparable to heterochroism in the Lepidoptera appeared a few times during the course of Morgan's extensive experiments with the Dipteron *Drosophila ampelophila*. He obtained new mutations which bred on Mendelian lines and showed the same kind of sex-limited inheritance as occurs in man in the case of colourblindness.

These mutations affected the size and shape of the wings and were of three kinds, "rudimentary," "miniature," and "rudimentary-miniature."

In one instance an individual appeared with a normal long wing on the left and a "miniature" wing on the right side, in another there was a normal long wing on the right and a "rudimentary-miniature" wing on the left, and in two cases the wing on one side was intermediate and on the other "rudimentary." Descriptions and figures are given by Morgan in the *Zeitschr. f. Indukt Abstamm.* 1912, VII, p. 323.

It is particularly interesting that the same Mendelian characters have been shown segregated both with and without segregation of sex characters into opposite halves of the body in the same species *Acidalia virgularia*, and *Aglia tau*, and that heterochroism of almost identical nature has occurred in *Anthrocera trifolii* both without gynandromorphism and in conjunction with it. Heterochroism has also occurred both with and without gynandromorphism in *Psilura monacha* and ab. *eremita*.

Abnormalities occurring in uniovular (homogeneous) twins afford parallels to one form of gynandromorphism, and to heterochroism in the Lepidoptera.

It is well known that both members of a pair of such twins are usually alike in all respects, and that hereditary diseases affect both, as one would naturally expect, since they arise by separation of the first two cleavage cells, each of which then develops into a complete individual. In fact they are the product of the union of a single spermatozoon with a single ovum. To illustrate this point I collected a number of examples in man in the *British Journal of Children's Diseases*.

The best known exception to this rule is the free-martin in the ox, which affords a close parallel to the gynandromorphism of insects, in which the secondary sexual characters of the two sexes are segregated to the opposite halves of the body. Free-martins are of two kinds, male and female. The male free-martin of which a good many examples are

known is always one of a pair of uniovular twins, the other being a normal bull, whereas the other twin in the case of the female free-martin is a heifer.

The male free-martin usually resembles a spayed heifer in external appearance, the sex glands are testes usually devoid of spermatozoa, and the other internal sex organs are of predominantly female type. This form is the "heifer free-martin." The "steer free-martin," externally like an ox, but internally like the other form, is much rarer. The female free-martin has ovaries, but the genital organs are of predominantly male type.

Berry Hart (*Proc. Roy. Soc. Edinburgh*, xxx, p. 238) says that "the free-martin with a potent bull twin is the result of a division of a male zygote, so that the somatic determinants are equally divided and the genital determinants unequally divided, the potent going to one twin, the potent bull, the non-potent genital determinants to the free-martin." He offers a similar explanation for the female free-martin. The two forms of male free-martin may be explained by supposing that there is more than one factor for secondary sexual characters, and that the unequal division may affect all of them in one case and only some of them in the other.

In man I only know of one case, in which segregation of Mendelian unit characters, comparable to that which occurs in heterochroism of Lepidoptera, has happened. It is a case described by Nettleship of female uniovular twins, one of whom was colour-blind and the other normal. He gives incontrovertible proof that they really were twins of this kind.

According to Doncaster colour-blindness is recessive to normal vision and an explanation of its rare occurrence in females is given by Jenkins (*Journal of Genetics*, III, p. 121).

The best explanation of this unique case is that an unequal division of chromosomes took place at the first cleavage, so that the factor for colour-blindness was segregated into one cell, that for normal vision into the other. Instead of the result being an individual with one side colour-blind, and the other normal, the two cleavage cells became separated. Each half grew into a complete individual, the one colour-blind, the other normal, but in all other respects alike.

That it was not due to the loss of a character by a sudden mutation, as Lang thinks, is proved by the fact that the father was colour-blind, and came of a family many of whose members were similarly affected, and the mother's grandmother was probably colour-blind also.

*Gynandromorphs partly of male type colour, and partly of
aberrational colour limited to the female sex.*

It is well known that there is in some regions, notably in the New
Forest, a dark form, ab. *valesina*, of *Dryas paphia*, limited to the female
sex. In several species of *Colias* normally orange in both sexes there is
a white or lemon-coloured aberration also limited to the female. An
instance of this is the ab. *helice* of the common clouded yellow, *Colias
edusa*.

Of *Dryas paphia* many gynandromorphs have been taken. Most of
these are halved externally, but some show one or more patches of
female colour on the male side or *vice versa*. In others there is a coarse
mosaic arrangement of male and female pattern and colour. In a
considerable number of these gynandromorphs all the female parts of
the wing are of the dark colour of the ab. *valesina*.

The following will serve as examples of this. In Schultz's lists no
less than 20 halved gynandromorphs of *D. paphia* are given, in which
one half was male type and the other female ab. *valesina*. In addition
less symmetrical examples are recorded.

(*a*) Right forewing male, right hindwing male flecked with dark
colour of ab. *valesina*. Left forewing mixed patches of fulvous male
colour and female ab. *valesina*.

(*b*) Right side male *paphia*, left side male *paphia*, with a broad
streak of *valesina* colouring along the costa of the forewing and a small
streak in the hindwing. (*Iris*, 1913, XXVI, Coloured Plate, Taf. vii,
Fig. 4.)

(*c*) Male *paphia* on right side with patch of *valesina* colour on
forewing; left side wholly *valesina*.

Mr Newman tells me that from a *valesina* ♀ he generally obtains
60 ♂♂, 40 ♀♀ (20 type ♀ and 20 % *valesina* ♀).

Professor Punnett also obtained about 50 % ♂♂, and 25 % of each
of the ♀ forms.

Colias edusa.

(*a*) Left side male: right female ab. *helice*.

(*b*) Right side male: left female ab. *helice*.

Colias erate.

(*a*) Right male, left female ab. *pallida*.

(b)   Male orange colour except for some scales of female ab. *pallida*
on left hindwing, female antennae and female external genitalia on the
left side.

Colias myrmidone.

Left forewing male, the other three wings male with streaks of
female colour ab. *alba*: underside left forewing male, other three wings
wholly female ab. *alba*: abdomen male.

Colias electra.

Right side male type, left pale lemon colour (var. *aurivillius*).
Entomologist, 1891, XXIV, p. 216.

With regard to the genus *Colias* Gerould's experiments in breeding
C. philodice lead him to take the view that the white aberrational colour
is dominant over the typical yellow colour in the female, and the yellow
colour dominant over the white in the male.   He also considers that
almost all the white females are heterozygous for colour, and that homo-
zygous whites, male and female alike, almost invariably fail to develop.
The families of *C. edusa* reared by Frohawk, Harrison and Main (*Proc.
South Lond. Nat. Hist. Soc.* 1905–6, p. 75), Sharp (*Ent. Record*, 1914,
XXVI, p. 82), and Tatchell (*ibid.* p. 49) suggest that in this species too
orange males may be either homozygous for orange or heterozygous
(orange-white), but white females ab. *helice* are all heterozygous (orange-
white)   On this supposition gynandromorphs partly of orange male
colour and partly of female white colour might either be of the same
constitution for colour in both areas, i.e. heterozygous, or might differ as
the heterochroic females must do and have the orange portions homo-
zygous for orange and the white portions heterozygous.

It is possible that *paphia-valesina* gynandromorphs may be alike in
actual constitution as regards colour, though the male and female areas
are so strikingly different in appearance.

Ganoris napi.

(a)   Left side male, right female ab. *bryoniae.*

(b)   Wholly male except for part of left forewing which is ab.
bryoniae.

(c)   Right forewing male, other three wings ab. *bryoniae.*

The ab. *bryoniae* is evidently dominant to the type and limited to
the female sex.   Mr H. Main informs me that in his experiments males
from a *bryoniae* female crossed with *napi* females give all *napi* in F_1
and F_2, but male *napi* crossed with female *bryoniae* give all males *napi*,

and all females *bryoniae*. This appears to be a simple case of repulsion between the factors *B* and *f*. *Bryoniae* female would have the constitution *BbFf*, *napi* male *bbff* and *bryoniae* female would be a heterozygous dominant for both sex and *bryoniae* factors.

Melanargia galathea.

A remarkable and unique gynandromorph was exhibited at the South London Nat. Hist. Soc. in 1913. It was captured by the Rev. George Wheeler at Pont de Pieve, July 17, 1909, in the evening, and flew very clumsily. It shows mixed characters of type male and ab *lugens* female (Pl. XXI, figs. 3 and 4).

The ab *lugens* is very rare and the few I know of are all females. Figures are given in the *Entomologist*, 1873, VI, p 57, and the *Bull. de la Soc. Lépidopt. de Genève*, I, p. vi. If the aberration is ever met with in the male this specimen belongs to the previous group of heterochroic gynandromorphs. Gynandromorphs of this species are extremely rare.

The left antenna is black, but is malformed, being twisted and shorter than the right. The right antenna has grey scales on it.

The left forewing is black (ab. *lugens*) except for a streak of male colour running from base to margin, the left hindwing is wholly black. On the underside of the left forewing there is more normal colour of male type near the base, and some also on the underside of the left hindwing; otherwise the distribution of type colour of male and ab. *lugens* of female is much the same as on the upper side.

It appears to have two valves and an ovipositor.

For permission to describe and figure it, I am indebted to the captor.

HEREDITARY AND FAMILIAL NATURE OF GYNANDROMORPHISM.

There is no doubt that gynandromorphism is in some cases familial.

I have already referred to the four heterochroic gynandromorphs bred by C. W. Simmons from a pairing of *Hemerophila abruptaria* type with the melanic ab.*nigra*, and to the three heterochroic gynandromorphs, and one gynandromorph of purely type form of *Aglia tau* bred by Standfuss from ova obtained by crossing a type specimen with a melanic ab. *lugens*. This was a most interesting family showing one individual with segregation of sex characters only and three with segregation of sex characters and somatic characters. Harrison and Main bred seven

halved gynandromorphous *Amphidasys betularia* and a male with antennae almost simple, which may have had a female element in it, from one batch of ova. Twenty normal males and forty females were bred from the rest of the ova, but these refused to breed inter se, and, unfortunately, the strain was lost.

In a brood of hybrid *Selenia tetralunaria* ♂ × *S. bilunaria* ♀ reared by Mr E. B. Haynes in 1913, there was a great preponderance of gynandromorphous individuals, though this cross, like the reciprocal cross, usually produces only normal males and females, a fact which I have confirmed by dissection.

Two gynandromorphous *Phlebeius argus* (*aegon*) were taken by the same captor at Dover in 1858. They were exactly alike being predominantly female. The right side in both was smaller than the left, and thickly peppered with blue scales and androconia, the left side was larger and entirely brown as in the normal female. Gynandromorphs of this species are rare and no similar one has been described so that it is highly probable both came of the same parentage.

Two gynandromorphs of *Amorpha populi* were bred by Shuttleworth from the same lot of larvae in 1880. (*Entomologist*, 1880, p. 116.)

Two gynandromorphs of the same species were also bred, August 2nd, 1914, by Mr H. B. Williams from one batch of ova. Both parents were normal in appearance. One was perfectly halved, right side male, left female; the other was similar except for a small area of male colouration near the costa of the left forewing and another near the hind margin.

In the *Ent. Zeitschr.* XX, p. 241, there is a record of three gynandromorphous *Saturnia pavonia* of mixed type being bred from one batch of ova derived from a very much inbred strain. Two were predominantly male and one predominantly female.

Speyer records in the *Stett. Ent. Zeitung*, 1881, XLII, pp. 477–486, a similar family bred from a few larvae of *S. pavonia* found on a branch of *Salix aurita* near Wiesbaden. Five mixed gynandromorphs emerged, one predominantly male, three showing the character of both sexes equally, and one predominantly female. Of five dead pupae also three were gynandromorphous.

In Hymenoptera gynandromorphism is rare, especially in ants. Horace Donisthorpe up to this year (1914) could only collect a total of 31 cases, and yet of these two occurred in the same nest of *Anergates atratulus*. This must be more than a mere coincidence.

But far more convincing is the honey-bee *Apis mellifica*. In this species apart from one hive only 15 examples are known. In the

famous Eugster hive near Constance, hundreds were bred over a period of four years. These were all the offspring of one queen of the Italian race, which probably paired with a German drone. Von Siebold alone received more than 200 and dissected 87 and Menzel dissected 30 more. The gynandromorphs were of various forms, predominantly drone-like, half drone, half worker and predominantly like a worker (imperfect female). Four of these have been dissected and figured by Elsa Mehling.

One of the *Anergates atratulus* throws a little light on the psychology of these creatures. It first tried repeatedly, but in vain, to pair with a female, and later on a male tried in vain to pair with it.

It falls into the group of primary somatic hermaphrodites having a testis but no ovary. The external genitalia were on the right of female type but imperfect, on the left of male type. The second was similar but had external genitalia of male type.

The Eugster bees were some of them genetic hermaphrodites of different forms, others secondary somatic hermaphrodites of different forms.

Hereditary Gynandromorphism probably of Indirect Descent.

Mr L. W. Newman for some years has bred a number of gynandromorphous *Amorpha populi*; in successive years he bred 17, 14, 11 and 2 out of totals of 2000, 1500, 1000 and 800 approximately. This year I have bred three from 500 of his pupae. This gives about 1 ⁒ of gynandromorphs. Newman has also bred a good many hybrid *A. ocellatus* ♂ × *A. populi* ♀ in recent years, using females of *A. populi* from this race. Amongst these hybrids no less than five have been halved gynandromorphs. Only three such examples have been recorded previously. Their occurrence is almost certainly due to the crossing with his gynandromorph-producing strain and not connected with the fact that the female hybrid is always replaced by a peculiar form of symmetrical gynandromorph. In 1914–5 one of these families produced 13 ♂♂, three symmetrical gynandromorphs and one halved gynandromorph (L. ♂, R. ♀). Another in 1912, 25 ♂♂, ten symmetrical gynandromorphs and two halved gynandromorphs.

Two of his gynandromorphous *A. populi* which hatched about the same time and were almost certainly from the same batch of ova showed heterochroism deep pink (?ab. *rufescens*) female and blue-grey (type) male halves.

Both are in Mr Bright's possession.

In Lepidoptera Speyer calculates that about one in 30,000 is a gynandromorph, and though there is little doubt that they occur more frequently in this species, the proportion is probably not higher than one in 5000 to 10,000.

I have dissected eight of these gynandromorphous *A. populi*, three of which are figured (Pl. XXI, fig. 5) and diagrams of their genital apparatus are also given (Diagrams *a—i*).

The following are descriptions of these individuals.

(1)   (Diagram *a.*)   Pl. XXI, fig. 5 *a*.   Left side ♂.

Right side predominantly ♀ (both wings partially crippled).
Colour: the same shade of grey on both sides.
R. antenna intermediate.
R. palpus ♀.
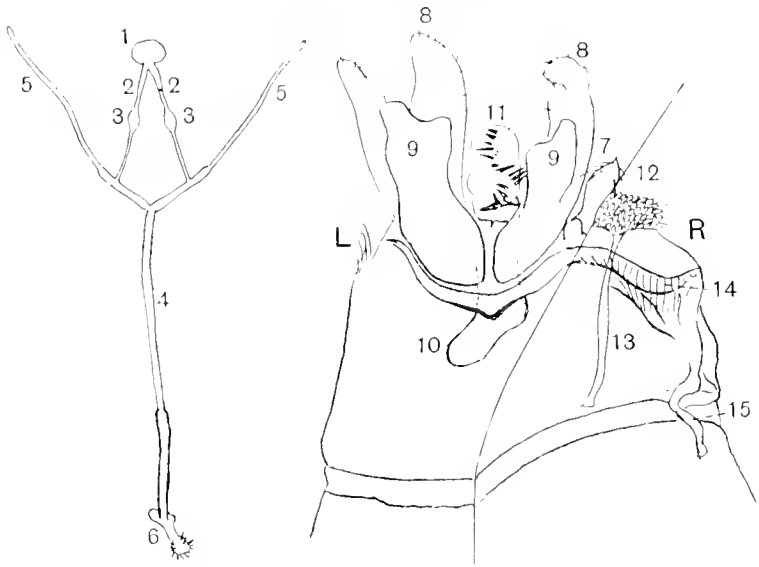R. half of thorax smaller and with shorter hair.

Diagram *a*.   *Amorpha populi* (Pl. XXI, fig. 5 *a*).   Left side ♂.   Right side predominantly ♀ (both wings partially crippled).   Right antenna intermediate.   Right palpus ♀. Right half of thorax smaller with shorter hair.

1, Testis; 2, vas deferens; 3, vesicula seminalis; 4, ductus ejaculatorius; 5, glandula accessoria; 6, penis; 7, uncus; 8, valves (deformed); 9, sacculus; 10, penis; 11, vesica of penis with cornuti; 12, half ovipositor; 13, directing rod of ovipositor; 14, ostium bursae; 15, rod of ninth segment. Bursa copulatrix absent. Line gives division between ♂ and ♀ organs.

Internally two testes with complete accessory male organs, female organs entirely absent.

External genitalia: 10th segment completely halved, 9th segment half male, half female. The male (left half) shows a perfect penis and ringwall, two valves and sacculi, the right valve being imperfect.

The female half shows a thickened area of chitin, the ostium bursae and bursal neck, but no bursa copulatrix. The rod is also present.

(2) (Diagram b.) Pl. XXI, fig. 5 b. Imperfectly halved and uniform in colour.

Left side predominantly ♂.

Right side predominantly ♀.

Left antenna ♂, right ♀, both palpi ♀.
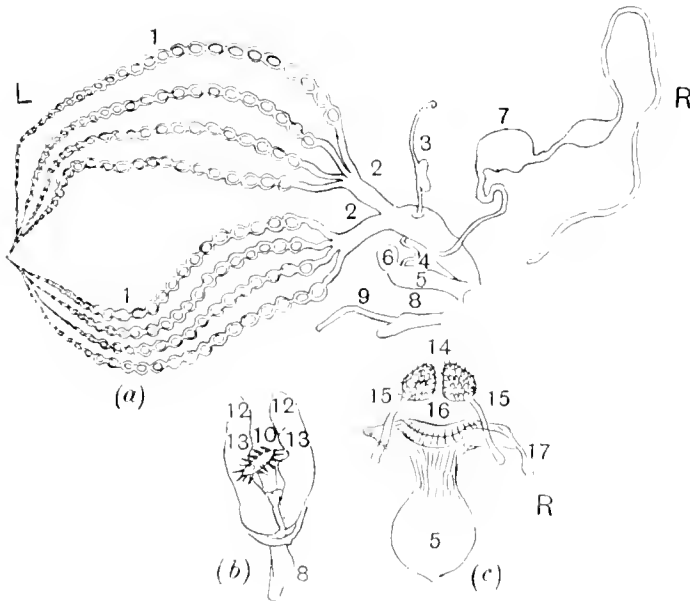
Diagram b. *Amorpha populi* (Pl. XXI, fig. 5 b). Imperfectly halved. Left side predominantly ♂. Right side predominantly ♀. Palpi ♀. Right antenna ♀, left antenna ♂.

1, Ovary; 2, oviduct; 3, receptaculum seminis = spermatheca; 4, ductus seminis (bursae); 5, bursa copulatrix; 6, caput bursae; 7, cement gland; 8, penis; 9, ductus ejaculatorius; 10, vesica; 11, ringwall; 12, valve (deformed); 13, sacculus (deformed); 14, ovipositor; 15, rods of ovipositor; 16, ostium bursae; 17, rod of ninth segment.

Internally two ovaries, oviducts, spermatheca, one cement gland (malformed), ductus bursae, and a small bursa copulatrix with caput are present. The male organs are represented by a small piece of ductus ejaculatorius ending blindly.

There is a complete set of external genitalia of female type, except that the rod of 9th segment on the left side is missing. The male portion was attached to the broken chitin, as shewn in the diagram, and the valves imperfectly formed were contained within the abdomen (the pupal condition). The penis and ringwall were well formed.

(3) (Diagram c.) Pl. XXI, fig. 5 c. Perfectly halved in all external characters and different in colour on the two sides (heterochroic).
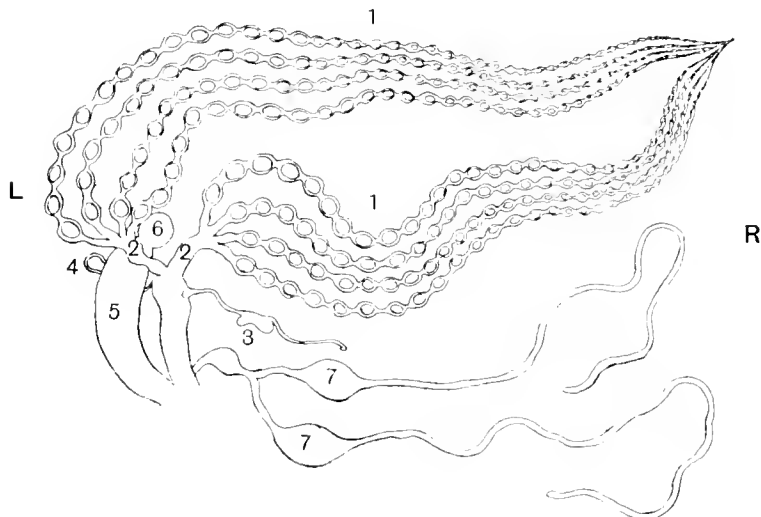

Diagram c. *Amorpha populi* (Pl. XXI, fig. 5 c). Perfectly halved in external characters and differing in colour on the two sides. Right side ♂, left side ♀. External genitalia not examined.

1, Ovary; 2, oviduct; 3, receptaculum seminis; 4, ductus seminis (ductus bursae); 5, bursa copulatrix; 6, caput bursae; 7, cement gland.

Right side ♂, left side ♀.

Internally there were two ovaries, oviducts, spermatheca, two perfect cement glands, ductus bursae and bursa copulatrix with caput. The external genitalia were not macerated, but a valve could be seen on the right side with the penis.

(4) (Diagram *d.*) Perfectly halved and of the same grey colour on both sides: wings not completely expanded.

Left side ♂, right side ♀.

Internally there were two ovaries, one with only three follicles, oviducts, spermatheca, cement gland and bursa copulatrix with caput. The ductus seminis was absent. External genitalia: 10th segment wholly female, 9th half female, half male, the latter part showing two valves and sacculi and a penis.
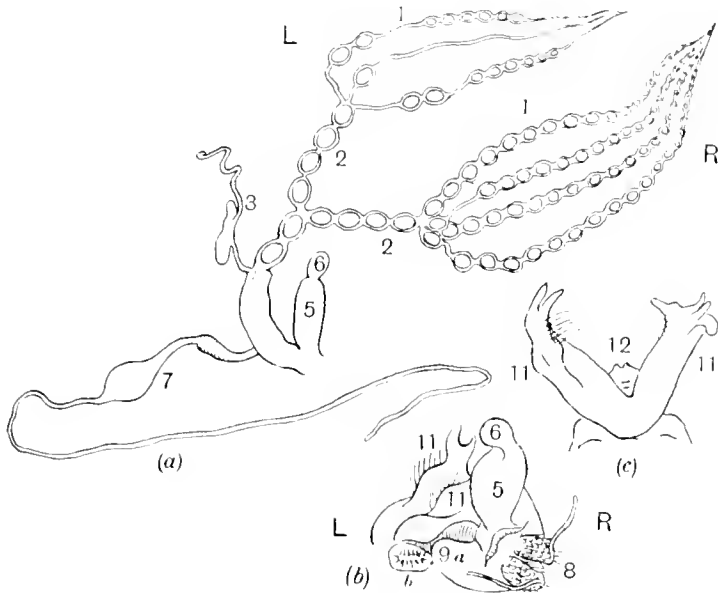

Diagram *d.* *Amorpha populi* (imperfectly expanded wings). Perfectly halved in external characters. Left side ♂, right side ♀.

1, Ovary; 2, oviduct; 3, receptaculum seminis; 4, ductus seminis (absent); 5, bursa copulatrix; 6, caput bursae; 7, cement gland (single); 8, ovipositor and directing rods; 9, penis (*a*) small and malformed aedoeagus, (*b*) vesica and cornuti; 11, valves (left malformed); 12, ringwall.

(5) (Diagram *e.*) Perfectly halved and the same colour on both sides.

R. side ♂, L. side ♀.

Internally there were two ovaries, one with only three follicles, and both containing very few small ova. There were oviducts, spermatheca and one cement gland. The ductus bursae (seminis) and bursa

copulatrix were absent. There were no male organs internally. External genitalia: on left side a perfect half ovipositor and rod, on right a very small half uncus (10th segment); on left side the ostium bursae was present and the rod, on right two imperfect valves, no gnathos and no penis (9th segment).
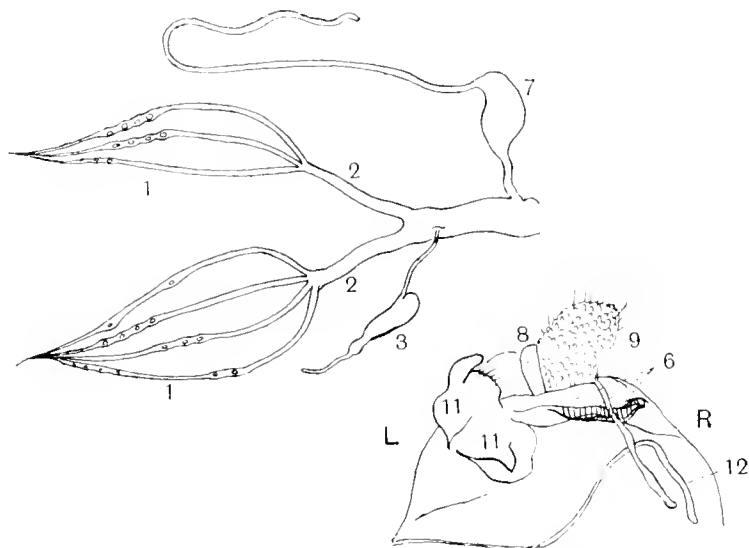

Diagram *c*. *Amorpha populi* (perfectly halved in external characters). Right side ♂, left side ♀. External genitalia show right side female, left side male with reduplication of valve and sacculus. Penis, bursa copulatrix, ostium bursae, ductus seminis, and one cement gland absent.

1, Ovary; 2, oviduct; 3, receptaculum seminis; 4, ductus bursae (absent); 5, bursa and caput (absent); 6, ostium bursae; 7, cement gland; 8, half uncus; 9, half ovipositor and rod; 10, penis (absent); 11, valves (malformed and both placed on male side of abdomen); 12, rod of ninth segment.

(6) (Diagram *f*.) Perfectly halved, pale buff colour on both sides. R. ♂, L. ♀.

Right side: a testis, yellow in colour, with four follicles full of spermatozoa, a vas deferens, vesicula seminalis, and ductus ejaculatorius. The testis lay in close contact with the commencement of the ovarian follicles.

Left side: an ovary with four follicles, a cement gland, ductus seminis, bursa copulatrix with caput: spermatheca absent.

External genitalia.

Right side a complete uncus and scaphium, two valves with sacculi, penis and ringwall. Left side half ovipositor and rod, ostium bursae, bursa, and rod of 9th segment.
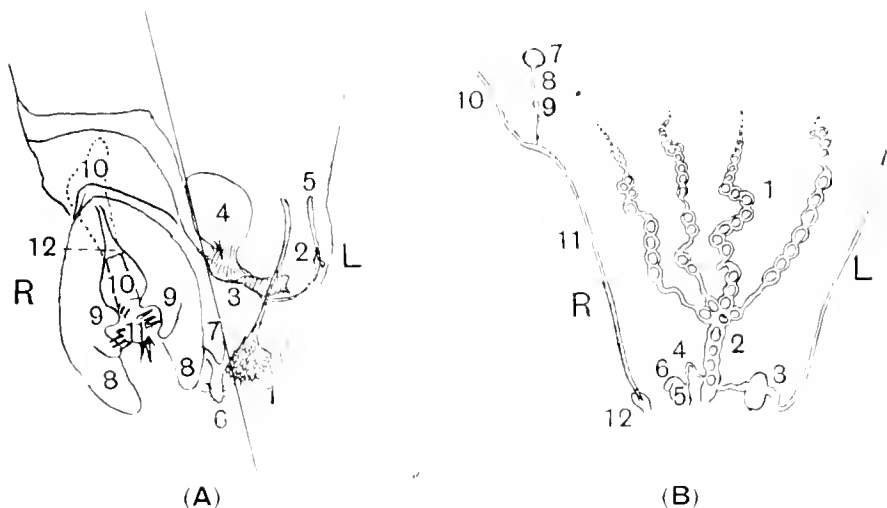

(A)   **(B)**

Diagram *f*. Halved gynandromorph, *Amorpha populi* (1915). Right side ♂, left side ♀. All internal organs perfectly halved. External organs halved.

- (A)   1, Ovipositor; 2, rod of ovipositor; 3, ostium bursae; 4, bursa copulatrix; 5, rod of ninth segment; 6, uncus; 7, scaphium; 8, valve; 9, sacculus; 10 penis; 11, vesica; 12, ringwall.

- (B)   1, Ovary; 2, oviduct; 3, cement gland; 4, ductus seminis (bursae); 5, bursa copulatrix; 6, caput bursae; 7, testis; 8, vas deferens; 9, vesicula seminalis; 10, glandula accessoria; 11, ductus ejaculatorius; 12, penis.

(7)   (Diagram *g*.)   ♀ Imperfectly halved, but completely pink. Head perfectly halved.

L. ♂, R. ♀.

Thorax smaller on right side (♀).

Wings equal in size and shape and like those of male, though some females have wings of this shape.

Abdomen fuller on right side.

Internally there was a testis, yellow in colour, on the left, with four follicles full of spermatozoa, lying against the lower part of the ovarian follicles. The testis had its vas deferens, vesicula seminalis, glandula accessoria, and ductus ejaculatorius. There was a second glandula accessoria, vas deferens, and vesicula seminalis, the vas being attached to the upper end of the common oviduct.

On the right there was an ovary with four follicles, oviducts, and cement gland.

Spermatheca, ductus seminis and bursa copulatrix were entirely absent.

External genitalia: those of a normal male, but displaced to the left of middle line, as if by female chitin representing the undeveloped female organs.
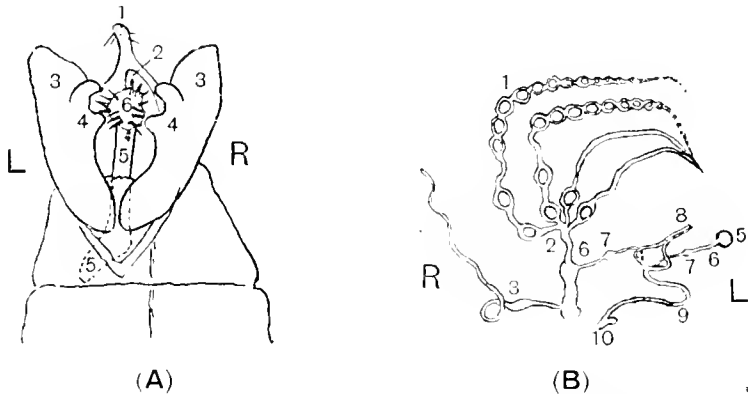

(A)   (B)

Diagram *g*. Gynandromorph of *Amorpha populi* (1915). A pink specimen. Head perfectly halved, left ♂, right ♀. Thorax smaller on right side (♀ character). Wings equal. Abdomen appeared male but was fuller on right.

(A) 1. Uncus; 2, scaphium; 3, valve; 4, sacculus; 5, penis; 6, vesica of penis. No ♀ external organs but all ♂ organs are to left of mid-line.

(B) 1, Ovary; 2, oviduct; 3, cement gland; 5, testis; 6, vas deferens; 7, vesicula seminalis; 8, glandulae accessoriae; 9, ductus ejaculatorius; 10, penis.

Receptaculum seminis, bursa copulatrix and ductus bursae absent.

(8) (Diagram *h*.) Perfectly halved and buff on both sides.

L. ♂. R. ♀.

Internally a testis, yellow in colour, with four follicles full of spermatozoa, vas deferens, vesicula seminalis, glandula accessoria and ductus ejaculatorius on the left: on the right an ovary with four very poorly developed follicles, only one containing more than a single ovum, oviduct, cement gland, and bursa copulatrix with caput. There was no spermatheca or ductus seminis.

External genitalia.

10th segment: on left side a small uncus, and scaphium; on right a half ovipositor with rod.

9th segment: on left, a penis, ringwall, two valves and sacculi; on right, ostium bursae, bursa and rod.
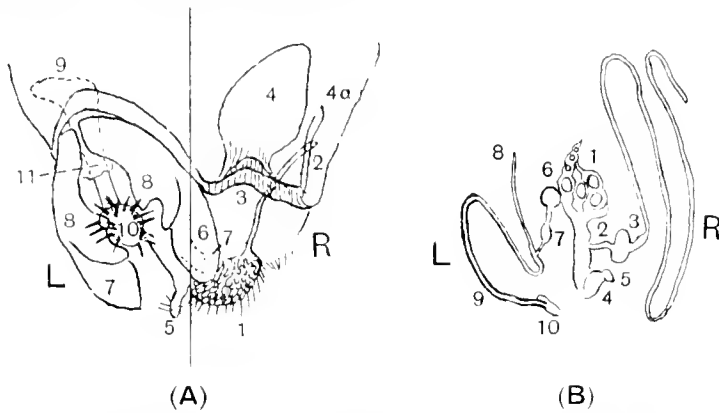

(A) (B)

Diagram *h*. Halved gynandromorph, *Amorpha populi* (1915). A buff specimen (colour same both sides). Left ♂, right ♀. Almost perfect halving internally and externally.

(A) 1, Ovipositor; 2, rod of ovipositor; 3, ostium bursae; 4, bursa copulatrix; 4*a*, rod of ninth segment; 5, uncus; 6, scaphium; 7, valve; 8, sacculus; 9, penis; 10, vesica of penis; 11, ringwall.

Vertical line divides ♂ from ♀ part except part of a valve and scaphium (♂ organ).

(B) 1, Ovary; 2, oviduct; 3, cement gland; 4, bursa copulatrix; 5, caput bursae; 6, testis; 7, vesicula seminalis; 8, glandula accessoria; 9, ductus ejaculatorius; 10, penis.

(9) (Diagram *i*.) Halved. L. ♂, R. ♀.

External genitalia.

10th segment: left side, uncus and scaphium; right side, half ovipositor and rod.

9th segment: left side, penis with ill-developed aedoeagus, perfect vesica and cornuti, two valves and sacculi perfectly formed; right side, small ostium bursae and bursa, and rod.

Hereditary gynandromorphism has also been noticed by other observers.

Lang with inbred *Aglia tau* obtained in successive years 1, 2, 2, and 1 gynandromorphs out of totals of 800, 988, 1109, and 581 respectively, or approximately one gynandromorph in 600 (·17 /).

Rowland-Brown, quoting Oberthür, states that at Dompierre in France halved gynandromorphs of the common blue, *Polyommatus icarus*, are fairly numerous. His collector caught 27 of these in a single season.

The ground on which these blues occur is a small area and the other blues found there, i.e. *Agriades coridon* and *A. thetis*, do not produce gynandromorphs. The species is one which does produce gynandromorphs with some frequency, but never in such large numbers in one locality.

Pantel and Sinéty have for years bred many generations of the Phasmids, *Dixippus morosus* and *Dixippus* sp. unknown, without any loss of fertility or other sign of enfeeblement.
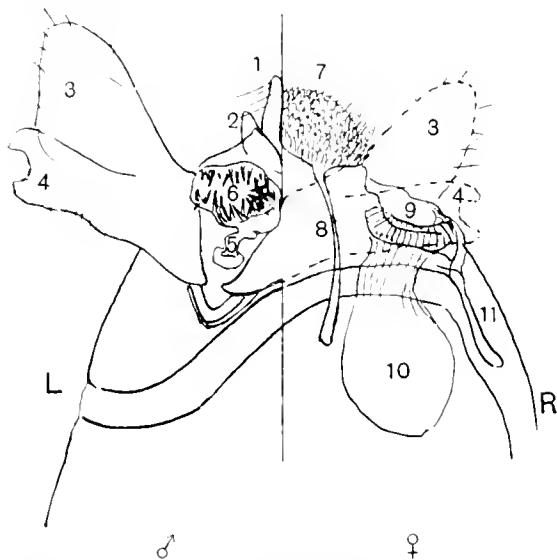

Diagram *i*. External genitalia of a perfectly halved *Amorpha populi*. The right side is
   purely female with half ovipositor and rod, small ostium bursae and bursa copulatrix.
   The left side is male with half uncus and small malformed penis. It shows redupli-
   cation of the valve and sacculus.

♂. 1, Uncus; 2, scaphium; 3, valve; 4, sacculus; 5, penis (small and ill-formed aedoeagus);
   6, vesica of penis with cornuti.

♀. 7, Ovipositor (half); 8, rod of ovipositor (tenth segment); 9, ostium bursae; 10, bursa
   copulatrix; 11, rod of ninth segment.

Line divides ♂ from ♀ organs, both valves can be seen to arise from left side.

From a large batch of eggs of *D. ?* sp. amongst many normal females were two males and one halved gynandromorph. The same thing also occurred several times with *D. morosus*. In 1908 six gynandromorphs, showing the internal and external characters of both sexes, were bred, though the hermaphroditism was not such that both kinds of apparatus were capable of functioning. Most died young, but those which reached

maturity laid a variable number of ova, if they possessed one or two ovaries.

The authors regard this as an attempt to produce a bisexual generation, and this seems to be the most likely explanation. In these parthenogenetic insects the ova undergo no reduction divisions until a bisexual generation is formed.

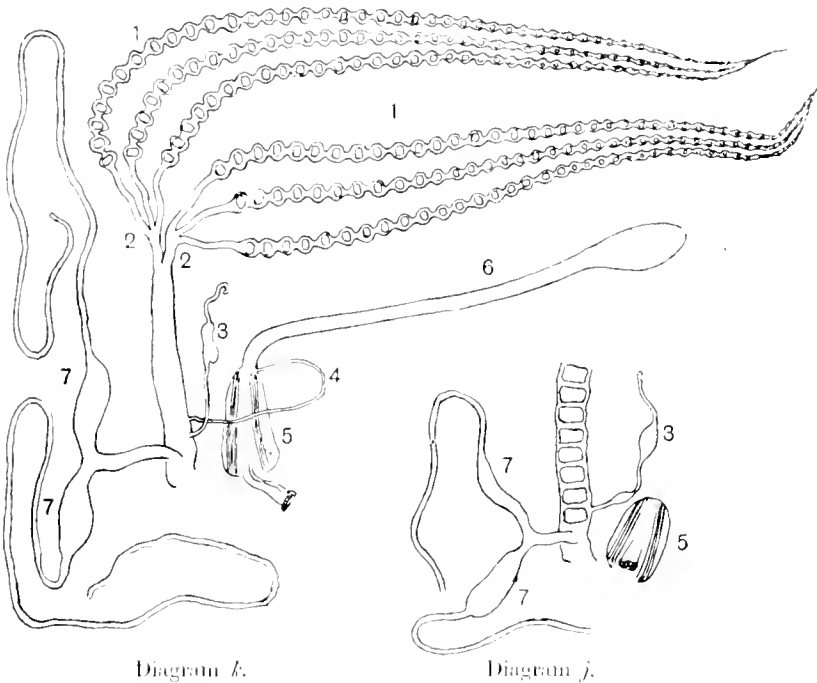An error of meiosis might give rise to a halved gynandromorph.

Diagram *k.*   Diagram *j.*

Diagram *j.* *Agriades coridon.* Caput bursae, ductus seminis absent. One cement gland atrophic.

Diagram *k.* *Agriades coridon.* Three ovarian follicles instead of four on each side.

1, Ovary; 2, oviduct; 3, receptaculum seminis; 4, ductus seminis; 5, bursa copulatrix; 6, caput bursae; 7, cement gland.

Hereditary Gynandromorphism probably of Direct Descent.

Even more remarkable is the race of *Agriades coridon*, which inhabits a small isolated range of chalk downs in North Hertfordshire.

There are other isolated chalk hills to the north-east and to the west, also inhabited by *coridon*. In the Hertfordshire locality females always greatly exceed males in number, sometimes as many as ten or

twenty to one. In addition there is a good deal of blue scaling on the hindwings of many of the females, and in a certain percentage the hindwings are brilliantly blue and there is a large patch of blue at the base of the forewings. This is the var. *semisyngrapha*. On the neighbouring downs this variety is absent or very rare indeed, and the sexes are equal in number.

Amongst the females taken in 1912 were a few which had the wings on one side smaller than those on the other and were dusted with blue scales on the small side. The orange lunules were also smaller on the small side. In 1913 more than 80 similar specimens were taken, and in 1914 more than three dozen.

I carefully dissected seven of these, including one with the right forewing almost entirely blue, almost as blue as a male (Pl. XXI, fig. 6), and found no trace of male organs, neither testes, nor internal secondary sexual organs, nor external armature. Indeed except in two of them the female organs were perfectly formed and symmetrical, the ovaries were large and full of eggs. In one the bursa copulatrix was defective, the caput bursae, a very large and elaborate structure in this species, being absent; the ductus seminis (ductus bursae) was absent, and one cement gland was atrophic (Diagram *j*). In the other there were only three strings of ova in each ovary instead of four (Diagram *k*).

On examining the wings I found that all seven showed in addition to blue scales, which might belong to either sex, scales of two kinds which are found only in the male, the pale blue coarse hair scales, and the androconia or battledore scales. Neither of these is ever found in females, neither in the bluest *semisyngrapha* nor even in the completely blue aberration *syngrapha*. Androconia are supposed to be sexual scent scales, and are structurally quite different from any scale found in the female. The presence of one of them is sufficient to establish the existence of a male element.

In 50 which I examined afterwards to confirm this discovery, I found androconia in every one and male hair scales in the majority.

In a specimen taken on the same hill by the Rev. G. H. Raynor in 1910, there is a similar state of affairs, but the right forewing with the blue scaling is very minute, measuring 7 mm., whereas the left measures 15 mm., the right hindwing is a little smaller than the left and wedge-shaped white areas, blue scales, and the lunules are of a different colour from those on the other side (Pl. XXII, fig. 7). With the microscope the blue scales of male type were seen to be abundant on the aborted wing, and amongst them were androconia.

The external genitalia were of ordinary female type.

One in the Hodgson collection at Cambridge shows a very slight diminution in the size of the right forewing and no additional blue scales or androconia, but the right hindwing is much reduced and has many blue scales and androconia.

One of these partially halved gynandromorphs is an example of the ab. *semisyngrapha*, but both wings are smaller on the left side, and have numerous additional blue scales with androconia and male hair scales (Pl. XXII, fig. 14 *a*).

The following are the only exceptions to this peculiar halved arrangement in these gynandromorphs. In one specimen diffuse blue scaling occurred all over both forewings, and to a slight extent on the hindwings. More blue scales were seen on the right side, and this was a little smaller than the left. Androconia were seen on both forewings, though more numerous on the right. The external genitalia were of purely female form. There were two ovaries and a perfect bursa copulatrix, but, as it was a dried specimen, finer details were destroyed by softening the abdomen (Pl. XXII, fig. 9).

Mr P. M. Bright has a specimen very similar, which has androconia and male hair scales on both forewings, and Mr Pickett has one which is very blue but shows only a few androconia on each forewing. It is evidently a bluish female with the addition of a slight male element on both sides (Pl. XXII, fig. 8). Another interesting specimen, possibly bilaterally gynandromorphous, is in Mr Pickett's possession. There is great asymmetry, and on the small side (left) are no blue scales, the fringe is almost unspotted on the forewing, and no androconia can be seen, whereas on the big side (right) there is a group of blue scales, male hair scales, and androconia close to the central spot (Pl. XXII, fig. 10). A specimen in Mr Bright's collection is equal in size on both sides, but the whole of the right forewing and the upper third of the hind-wing are thickly covered with blue scales. Androconia are scarce. On the under side the peculiar scales usually confined to the basal area run right out to the apex, forming a band along the costa.

A remarkable unequal female, which I have examined, is in Mr Pickett's collection. It has only one blue scale on the left or small side and none on the right or big side, except for the basal scales present in all females. (Pl. XXII, figs. 11 and 12.)

The lunules are much larger in both the wings on the larger side, corresponding to ab. *aurantia* Tutt, and typical on the smaller side. The under side is very asymmetrical, the larger side being ab. *parisiensis*

and the smaller typical, and the corresponding spots on the two sides are nearly all unlike in size and shape. There is also an abnormal extension of the black and the green basal scales, well seen in the figure (Pl. XXII, fig. 12). This is probably an example of heterochroism, though the spotting of the undersides of blues is notoriously liable to some asymmetry. Many of these unequal gynandromorphs show some degree of asymmetry of the under side, and one in my possession is typical on one side, ab. *parisiensis* on the other (Pl. XXII, figs. 12 *a* and 12 *b*).

Whether Mr Pickett's specimen is gynandromorphous as well as heterochroic I cannot decide with certainty.

In some the male scales are chiefly situated near the base, in others near the apex, and in others along the costa or along the hind border of the wing. In some, small patches occur, which if cut out from their surroundings would be identified as a piece of wing from a male (Pl. XXIII, figs. 14, 15 and 16). I have one where most of the blue scales are near the apex and the apex is the part most obviously reduced in size (Pl. XXII, fig. 13), but a better example is in Mr T. W. Hall's collection. This is purely female in appearance except for a small collection of blue scales close to the right apex, perhaps 50 in all, but amongst them there are several androconia. There is a slight blunting of this apex, but no diminution of size in the rest of the wing.

Under the microscope the arrangement of scales in these specimens is seen to be very irregular, in some the blue scales are largely single, in others they occur in small or large groups (Pl. XXIV, fig. 17).

The genitalia of six, in addition to those dissected completely, have been examined and all show external armature of purely female type. Ovaries full of ova and a well-formed bursa copulatrix could be recognised. They could therefore almost certainly produce fertile ova in a majority of instances.

This remarkable race of gynandromorphs is peculiar in that the admixture of male tissue with female appears to cause invariably a reduction in size, though the male *coridon* is considerably larger than the female and the reverse effect would be expected. Gynandromorphs of this species are very rare in other localities, only six being recorded, and are for the most part of the halved or predominantly male form.

In addition to these undoubted gynandromorphs a very small number of females are found in which one or more streaks of blue occur, sharply

defined from the prevailing brown of the rest of the wing. Similar specimens have been met with elsewhere, but only very rarely.

These blue scales are either like those of a male in shape or those of the bluest *semisyngrapha*, namely smooth-edged, or slightly serrate like the majority of scales on slightly blue females. But in none of them, which I have examined, do male hair scales or androconia occur.

I have investigated the internal and external genital organs of one, and they were purely female, the external genitalia of another showed normal female characters. A third similar specimen examined by Dr Chapman showed purely female organs, internal and external.

It is doubtful whether these streaks of male colour are really streaks of true male tissue.

The only specimens resembling the Royston examples are two in number, one in Mr Bright's collection taken at Tring in 1899, and one in the Hodgson collection at Cambridge, labelled Bevingdean 7. 9. 1888. In the latter the blue scaling is profuse over the small or right side, and androconia occur on both fore and hindwings.

A great contrast is presented by a gynandromorphous *Polyommatus icarus*, taken in County Clare in June 1914. This is predominantly female in appearance, though of the blue (approaching ab. *coerulea*) form. It has small streaks of brighter blue (male colour) on one fore-wing and both hindwings, and on these androconia are as abundant as on similar areas of wing in a normal male. The abdomen is female in shape, but the external genitalia are purely male in form and in all respects normal (Pl. XXIV, fig. 18).

The only proof of the directly hereditary nature of the condition in Lepidoptera is that given by Wiskott, who quotes a letter from Schutze, saying that a brood of *Lymantria* (*Ocneria*) *dispar*, bred from ova found in the winter, produced 83 pupae. Three gynandro-morphs, males in all external characters except for splashes of female colours on the wings, were bred. The other imagines were normal males and females.

One of these gynandromorphs paired with a normal female of the same brood, and 65 pupae resulted from a large batch of ova. Nearly half the ova were infertile. From these pupae two gynandromorphs resembling the male parent were bred; the other imagines were normal. One of the gynandromorphs paired with a normal female of the same brood and a small batch of ova was laid, 25 % smaller than normal. Most of the resulting larvae died in their first and second instar,

probably as the result of excessive inbreeding, and only three pupae were obtained, from which three normal females emerged.

The primary and secondary sexual organs of these gynandromorphs were presumably purely male as in the figure given by Wenke of a similar specimen. They were probably secondary somatic hermaphrodites of male type, comparable in their genitalia with the female secondary somatic hermaphrodites of *Agriades coridon* previously described.

From this evidence it is impossible to doubt that in the French and Hertfordshire localities races of the butterflies *A. coridon* and *P. icarus* occur in which gynandromorphism is hereditary, in the former by direct or indirect descent, in the latter probably by direct descent. Indirect descent is most probable in the case of the French halved *icarus*, for it is physically impossible for most gynandromorphous insects to produce offspring. It is true that Scopoli in his book, published in 1777, records an instance in the following terms:

"*Phalæna pini* Linn. Larvæ binæ, intra unicum, quem pararunt, folliculum, mutatæ sunt in unicam Pupam, unde Animal dimidia corporis parte masculum; antenna plumosa, alisque binis majoribus; alia vero femineum; antenna setacea, alisque binis minoribus. Quod vero mirabilius, pars mascula emisso pene fecundavit ovula femineæ, quæ deposita perfectas larvas protulerunt."

Though his explanation of self-fertilisation is impossible, the ova may have developed parthenogenetically as sometimes occurs in this group, or the insect may have paired with a male of the same species.

That the latter is not impossible is proved by the observation of Dr Cloquet. He took a pair of *Dryas paphia* on the wing, the male paired with a gynandromorph. This was a halved example, and though no internal examination was made, the external genitalia were of both sexes.

Edward Newman records a gynandromorph of *Liparis* (*Lymantria* or *Ocneria*) *dispar*, with male antennae but otherwise of female appearance. This remained paired with a normal male for three hours. The abdomen contained no ova, though the structures were of female character.

Wenke also records the discovery of halved gynandromorphs of *Parnassius apollo* and *delius*, each with the sphragis or abdominal pouch present, proving they had paired with males.

A water beetle, *Dytiscus latissimus*, has also been taken by Altum

paired with two males. Though largely male on the right and female on the left, it was a mixed gynandromorph.

The Engster gynandromorph bees were repeatedly observed to pair with normal males.

Wenke gives other instances.

But even when copulation is possible, it by no means follows that fertile ova can be produced in genetic and primary somatic hermaphrodites; it must be an occurrence so rare as to be negligible. In the secondary somatic hermaphrodites, on the contrary, fertile ova may be expected, whether they are of male or female type.

Amongst the *Lymantria dispar* L. × *Lymantria* var. *japonica* Motsch., the more male of the male gynandromorphs and weibchen-männchen, and the more female of the female gynandromorphs possessed the sexual instincts of males and females respectively and were fertile. The more intermediate specimens had loss of sexual instinct.

The most complete example of hereditary gynandromorphism is that recorded by Olga Kuttner in Cladocera.

A young *Daphnia pulex* was found wild which had some male characters on one side, though two ovaries and no testes were present. Twelve broods were produced by parthenogenesis and in nearly all of them there were some individuals, which showed mixed gynandromorphism. Male characters were present to a varying extent, and were chiefly observable in the taste antennae and first foot; in some, male characters were present on both sides, but in the majority they were confined to one side.

Nearly all were predominantly female and only possessed ovaries.

Four generations were obtained, and in all of them similar specimens continued to appear.

In the last seven broods produced by the original specimen there were 104 individuals, 79 female, 24 gynandromorphous, and 1 male (24 % gynandromorphs).

In the whole of the third generation there were 350 individuals.

Normal females	...	...	...	...	253 = 72·3 %
Gynandromorphs with ovaries only			...		85 = 24·3 %
Gynandromorphs with testes only			...		3 = 0·85 %
Gynandromorphs with ovary and testis	...				3 = 0·85 %
Normal males	...	...	...	...	6 = 1·7 %

And in the fourth generation there were 80 individuals, of which 17 (21 %) were gynandromorphous.

Hybrid Gynandromorphs.

Gynandromorphism is far commoner amongst hybrids than amongst pure races of Lepidoptera.

The well-known hybrid hawk-moth, *Amorpha (Smerinthus)* hybr. *hybridus* Steph. (*A. ocellatus* ♂ × *A. populi* ♀) and *Amorpha* hybr. *operosa* Standfuss (*A. ocellatus* ♂ × *A. populi* var. *austati* ♀), gives males with a few gynandromorphs and no females. The gynandromorphs as a rule resemble females and are quite symmetrical. The internal organs according to Roepke are similar in both hybrids. Two ovaries are present much distorted and atrophic. The other internal sex organs were in part hypertrophied, in part atrophied, and in some portions were completely cut off from the rest. No male internal organs were present. Excellent figures are given by Roepke.

In the external genitalia there was a curious mosaic of male and female parts, male portions preponderating in some, female in others, with every degree of intermediate arrangement.

One hybrid *operosa* had a partially bifid uncus with two small patches of ovipositor inlaid upon one side and one patch upon the other. Burrows and Pierce find a similar arrangement in the numerous examples of hybrid *hybridus* they have examined, and I possess one showing the same features. Though a series could be prepared to show a transition from a preponderantly female to a preponderantly male type, in all cases the genitalia are very nearly symmetrical and therefore quite unlike most natural gynandromorphs. In some of these quite small islands of thick male chitin are found let into larger areas of thinner female chitin.

One male gynandromorph of hybr. *hybridus* was found by Roepke. It possessed two testes with normal male accessory structures and male external genitalia with the exception of two large areas of ovipositor replacing part of the undivided uncus. Males of these hybrids have testes, of normal or reduced size, but with no fully formed spermatozoa. The inner and outer genitalia are those of normal males.

Halved gynandromorphous examples of hybr. *hybridus* have been recorded by Birchall, Briggs, Schultz and Newman, but though the sexual characters are completely segregated, both halves show an equal admixture of the somatic characters of both parents. Such completely

halved examples probably arise in the same way as the rare halved gynandromorphs of other hybrids such as Standfuss' *Saturnia pavonia* ♂ × *S. spini* ♀ and halved gynandromorphs of pure species. They are very rare indeed.

The reverse hybrid, *A. populi* ♂ × *A. ocellatus* ♀, has only produced four imagines. The eggs are fertile but the larva fails to escape from the shell. Males and females are said to have resulted, and the one I have seen is a male in appearance.

Standfuss in his extensive experiments with the genus *Saturnia* (emperor moths) found that in primary hybrids gynandromorphs were comparatively rare, 2 in 4000, perhaps as rare as in *S. pavonia* itself but in secondary hybrids they were numerous.

Saturnia (*pavonia* ♂ × *pyri* ♀) ♂ × *S. pyri* ♀ gave five gynandromorphs out of eight imagines, *S.* (*pavonia* ♂ × *pyri* ♀) ♂ × *S. pavonia* ♀ gave 12 out of 54. Twenty broods of secondary hybrids mixed together gave 280 imagines with 27 gynandromorphous individuals.

In external appearance almost all the secondary hybrid gynandromorphs were predominantly female and showed a coarse mosaic arrangement, though in one or two a whole wing showed the secondary sexual characters of one sex only.

Unfortunately only those most like females were dissected and these all contained ovaries, many with few and ill-formed eggs. None contained testes or male sex cells in their ovaries. The external genitalia showed the characters of both sexes.

Harrison amongst several thousand primary hybrid *Bistoninae* found only one gynandromorph.

A second was bred by Mr Worsley-Wood. It is a specimen of hybrid *harrisoni*, Harrison, (*Ithysia zonaria* ♂ × *Lycia hirtaria* ♀), female in all respects except the left antenna which is male. But of Harrison's secondary hybrids the ten imagines bred were all gynandromorphs, and 50 pupae were also without exception gynandromorphous. Some of the imagines were predominantly male, others predominantly female, but none showed any approach to a halved condition and none examined were genetic hermaphrodites. The external structures showed a coarse mosaic arrangement of male and female parts. (*Vide* Plates in Oberthür's *Lépidoptérologie Comparée*.)

GYNANDROMORPHOUS MONGRELS.

Brake, Goldschmidt and others have produced very large numbers of gynandromorphs by crossing *Lymantria dispar* Linn. with its var. *japonica* Motsch.

Though the latter is sometimes considered to be a distinct species, it is almost certainly merely a larger and more deeply coloured variety. It exhibits the same differences from more Western races as many other Japanese insects such as *Papilio machaon* show.

In some families they appeared in very large numbers, in others they were entirely absent.

Three kinds of gynandromorphs were produced:

(1) Female gynandromorphs. These were like females in size and shape, with either a blending or a mosaic arrangement of male and female colour and pattern. They had two ovaries, and the other sexual organs, including the external genitalia, were female in character.

(2) Male gynandromorphs. These were like males in size and shape, but had patches or streaks of female colouring on the wings.

The sexual organs were like those of males except that in a few ova and oocytes were found with the spermatozoa and spermatocytes in the testes.

(3) Weibchen-männchen. These were exactly like males except for tiny specks of female colour scattered all over the wings. Their sex-glands were testes or were lobulated and contained oocytes and spermatocytes in all their follicles.

The external genitalia were modified, showing a transition from those of purely male type to a form closely approaching the female type.

Many of these gynandromorphs were fertile, the females functioning as females and the male gynandromorphs and weibchen-männchen as males, but in the more pronounced examples sexual instinct or sexual function was lost.

From this description it will be recognised that they differ very widely from ordinary gynandromorphs. All showed a close approach to bilateral symmetry in external characters, and in internal characters; none showed any approach to a halved arrangement.

The genetic hermaphrodites showed a form never met with in wild gynandromorphs, and no lateral genetic hermaphrodite was met with, nor did any unisexual individual occur with a single sex-gland.

THEORETICAL EXPLANATIONS OF GYNANDROMORPHISM.

Broadly speaking all the theories of gynandromorphism fall under four heads.

The first supposes that gynandromorphs are formed from a fusion of two ova or from a binucleate ovum, the second that they are formed by an abnormally dividing single ovum. The third is the Mendelian hypothesis based upon supposed differences in the potency of the sex characters in different races and species, and the fourth is that they are due to abnormal conditions occurring during the development of a normally fertilised ovum.

Scopoli foreshadowed the first theory by suggesting that his halved gynandromorphous *Phalaena pini* was formed by the fusion of two pupae in one cocoon.

Dorfmeister's idea is a little less crude. He suggested that two ova in one shell became fused, and then separated each uniting with half the other, and so producing two gynandromorphs. Much more probable is the view put forward by von Dönhoff in 1860. It was advanced to explain social hymenopterous gynandromorphs and depends on the belief of Dzierzon that all fertilised ova in these insects produce females or workers, and all unfertilised ova produce drones by parthenogenesis. That this is not universally true does not disprove von Dönhoff's theory. He supposed that these abnormal insects are produced from an egg with two yolks, one fertilised and one unfertilised. These fuse and form a single individual, the fertilised part forming part of a worker, and the unfertilised part of a drone. Boveri and others also support this view. It might be applied universally on the further supposition that if one nucleus of such an egg is fertilised the other will be stimulated to commence cell divisions by the spread of chemical bodies from the fertilised half. In view of Loeb's experiments on artificial parthenogenesis this is not very improbable.

It is disproved by the existence of perfect halved gynandromorphous hybrids, both sides of which show equal admixture of the characters of both parents.

Doncaster has recently suggested that a gynandromorph is produced by the fertilisation of each of the nuclei of a binucleate ovum by a separate spermatozoon. He has proved the existence of these binucleate ova and has actually proved the conjugation of a separate spermatozoon with each, and seen the resultant mitoses. The theory is a fascinatingly

simple one. It would explain the cases where one sex preponderates by supposing that one half develops less rapidly than the other. It explains the occurrence of heterochroic gynandromorphs. The two nuclei of the ovum may be alike in constitution, but one spermatozoon may differ from the other. One may carry a dominant Mendelian character and the other a recessive.

It also explains the partial or complete doubling of the genital apparatus.

Familial and hereditary cases would be caused by the familial and hereditary production of binucleate ova.

Doncaster himself points out an objection, and that is that no gynandromorphs were produced from the broods in which he found binucleate ova. He also states that in the one case, in which it could be investigated, the two zygotes of the fertilised egg would both have produced males.

There are other difficulties. On his supposition one would expect that in broods, where heterochroic gynandromorphs were produced, there would be an equal number of individuals showing heterochroism without any gynandromorphism.

No such individuals were produced in these broods.

Another objection which may be brought forward is the regular occurrence of gynandromorphs in certain mixed races and hybrids. It is certain that binucleate eggs do not occur in the parent species in any numbers or gynandromorphs of pure race would be equally common.

Amorpha populi, for example, produces gynandromorphs quite commonly, perhaps 1 in 5000, but they should occur in half the individuals to suit Doncaster's theory. But as will be seen later these gynandromorphs probably arise in a different way from the halved examples.

More important is the objection that reduplications only occur in the genital apparatus, whereas they should occur quite as often in other parts formed near the mid-line, if a gynandromorph is really a fusion of two potentially complete individuals.

The halved gynandromorph of *Thaumetopoea pinivora*, Tr. (left male, right female), whose abdomen bifurcated into two equal parts each with a complete genital apparatus is probably an example of partial fission of the embryo comparable to the abcaudal duplication in mammals, which gives rise to dipygus and other monsters.

The theories, which suppose that a gynandromorph develops from a uninucleate ovum, differ in some respects.

Von Siebold, for instance, thought that in such cases one spermatozoon enters the egg instead of many. This is incorrect for, though polyspermy is very usual in Lepidoptera, only one spermatozoon is necessary and only one takes part in the actual process of union with the female pronucleus. Morgan supposes that two spermatozoa enter one egg, one uniting with its nucleus, the other developing alone. This is open to the same objections as von Dönhoff's theory, i.e. the existence of halved gynandromorphous hybrids, showing the characters of both parents on both sides equally.

Menzel's supposition is based on the phenomenal numbers of gynandromorph bees of the Eugster hive. He considered that the queen was malformed and that the ova progressed so slowly past the receptaculum seminis that cell division had already commenced before the spermatozoon entered the egg. A parthenogenetically developing egg of the honey-bee usually produces a drone, so those ova, which began to develop parthenogenetically and continued in a more normal way, produced bees, part drone, part worker.

Lang also thought that premature division of the egg nucleus occurred and that the resulting nuclei were fertilised by spermatozoa which were different in their characters.

In connexion with this subject the experiments of Herbst on sea urchins are interesting. He obtained hybrids artificially between *Strongylocentrotus* and *Sphaerechinus*, and these were intermediate in characters between the two parent species. But by treating the eggs for $1\frac{1}{2}$ hours with fatty acid before adding the spermatozoa, he obtained a hybrid very like the female parent. On examination of eggs so treated the nuclei were found to have undergone mitotic division and modification before the spermatozoa reached them. Paternal chromosomes were eliminated in this way. A few eggs so treated produced plutei with one half resembling the male and one half the female parent. This he regarded as due to irregular distribution of chromatin to the first two cleavage cells, one receiving too much paternal chromatin and one too little.

Boveri has produced sea urchins in one half of which all the chromosomes are purely maternal, in the other a mixture of paternal and maternal. From this observation he thinks gynandromorphs may be similarly constituted, and supports a modification of von Dönhoff's theory.

This phenomenon of hybridity in sea urchins obviously bears a resemblance to halved gynandromorphism. But that it is identical

appears to me to be disproved by the existence of gynandromorph hybrids, some halved, in which both the male and female portions show precisely similar mixture of characters derived from both parents.

The other theories rest largely on the supposition that sex itself is a Mendelian unit character.

This supposition is based on numerous breeding experiments in cases of sex-limited inheritance. In insects, with a few exceptions such as *Drosophila*, and in birds maleness appears to be a homozygous recessive and femaleness a heterozygous dominant. The character for sex is supposed to be carried by a special chromosome. Secondary sexual characters are probably also unit characters but are closely linked with the primary characters and it is thought that they are present in the same chromosome.

Breeding experiments by Brake repeated and amplified by Goldschmidt with various strains of *Lymantria dispar* Linn. and its larger and more strongly marked variety *Lymantria dispar* var. *japonica* Motsch. have produced large numbers of gynandromorphs of three kinds distinct in their external appearance and in their internal structure. These are female and male gynandromorphs and " weibchen-männchen."

These were always absent in certain crosses and present in definite proportions in others.

By making certain assumptions the numbers were found to follow Mendel's law.

Goldschmidt uses the following symbols :

F = female sex factor.

f = its recessive.

M = male sex factor.

m = its recessive.

G = the factor for secondary sex characters of female.

g = its recessive.

A = the factor for secondary sex characters of male.

a = its recessive.

The male factor M is more potent than the female factor F but the potency is such that two female factors FF are more potent than one male factor M. The relation between G and A is similar. For convenience Goldschmidt gives the following arbitrary values in figures:

$$A = 60, \quad G = 40, \quad AA = 120, \quad GG = 80.$$

He gives the following formulae for the two sexes:

The male = $FFMMGGAA$ or more correctly $(FG)(FG)(MA)(MA)$.

The female = $FFMmGGAa$ or $(FG)(FG)(MA)(ma)$.

The male gametes are all of one kind $(FG)(MA)$ and the female of two kinds $(FG)(ma)$ and $(FG)(MA)$.

In *Lymantria* var. *japonica* he considers that the relationship between F and M and between G and A is the same, but that each factor is of much greater potency than in *L. dispar*. For A in *japonica* he gives a value of 120 and for G a value of 80. The factors for *japonica* he writes in thick capitals (e.g. **F** in place of F, &c.).

According to this scheme the individuals constituted **GG**$A a$, **GG**Aa, **GG**Aa, **GG**Aa would be normal females, and those constituted **GGA**a, **GGA**a would be gynandromorphous females.

Gynandromorphous males would be constituted **GG**AA. Gynandromorphous females were produced in the broods, where such combinations of factors were possible, and in the expected numbers. Gynandromorphous males were not produced in one brood, in which they were expected, but in another they appeared in the expected proportion of one to every seven normal males.

In one brood no females were produced, all were males (408) or males with small specks of white sprinkled all over them (71) (weibchen-männchen). To explain their appearance he assumes that the potency of the sex factors F and M can be lowered by inbreeding. He regards them as the product of a *dispar* with the constitution $FFMm$, F and M being of unusually low potency, crossed with a *japonica* of the constitution **FFMM**. The weibchen-männchen were thus constituted F**FM**m and in them the great relative potency of the male factor obliterated the female almost completely.

Another cross between individuals constituted $FFMm$ and **FFM**M gave half normal females, F**F**Mm and FF**M**m, and half weibchen-männchen, F**FM**m and FF**M**m. Those with formula FF**M**m are unrecognisable from normal males in external appearance. Hence the apparent result of this cross is always 2 females : 1 weibchen-männchen : 5 males.

Even if the explanation of their gynandromorphous families given by these authors is correct and we accept the view that they are due to differences of potency in the factors for sex and secondary sexual characters and that inheritance of these follows the simple Mendelian laws, we cannot extend the explanation to cover all instances of

gynandromorphism. Such differences of potency must be very unusual for no other crosses between different local races have produced gynandromorphs in the same way as in the *Lymantrias*.

Even in a large majority of allied but distinct species these factors must have the same potency, for primary hybrid gynandromorphs are only produced with certainty in two instances: *A. hybr. hybridus* and *A. hybr. operosa*. For these and for the secondary hybrid gynandromorphs Goldschmidt's explanation is possible; but for ordinary halved gynandromorphs and the halved examples which are sometimes met with in *A. hybr. hybridus* and other primary hybrids, I think another explanation must be sought for. Even for the regular occurrence of primary and secondary hybrid gynandromorphs a more gross physical cause is probable. In different species the chromosomes often differ in number and in size, and it is known that fusion between corresponding chromosomes does not always occur in their hybrids. Such chromosomes may take no part in mitosis and may be unrepresented in the nuclei of the cells of the resultant individual. This probably causes the great differences in reciprocal crosses in somatic characters, and may also account for the very different sex proportions. It may also explain the regular occurrence of gynandromorphs in these hybrids.

This will remain in doubt owing to the infertility of these true hybrids, though, perhaps, some light may be shed by a study of the behaviour of the chromosomes in the mitoses of the hybrids of the genus *Amorpha*.

The great objection to Goldschmidt and Poppelbaum's theory is that it only explains the finer mosaic or coarser mosaic gynandromorphs. It does not explain the occurrence of halved examples or of lateral genetic hermaphrodites. In all the vast number of *Lymantria* gynandromorphs bred there was not a single one completely halved in external characters, nor was there one nearly completely halved. Whereas amongst the 32 wild *Lymantria* gynandromorphs recorded, although there are many resembling Goldschmidt's and possibly due to the same cause, there are no less than 16 completely halved examples, including at least one lateral genetic hermaphrodite. In other species halved or nearly halved examples are far commoner than the coarse mosaic and these again are commoner than the fine mosaic examples.

Now it is quite possible to produce a mosaic appearance or a blended appearance of somatic characters; for instance certain strains of black fowls crossed with white produce fowls with a mosaic of black and white, other strains produce a blended blue F_1 generation.

But one does not find any race producing an F_1 generation, white on one side and black on the other, even as an exceptional occurrence. Yet this should be the case if Goldschmidt is correct.

Again according to him inbreeding and crossing different races or species are the cause of all gynandromorphism, and it is certainly true that many have arisen in inbred races. But in the inbred races which have produced the heterochroic gynandromorphs there has been no evidence to show that there has been any alteration in the potency of the colour characters. They have remained completely dominant and completely recessive in further generations, as in Simmons' *abruptaria* The numbers too in most of these familial cases are too small to suit a simple Mendelian expectation.

The gynandromorphous birds and the case of twins published by Nettleship can scarcely be explained on his theory. If the heterochroic gynandromorphs arise as Goldschmidt and Poppelbaum believe, the mosaic areas formed of the colour and pattern of the two sexes, and those formed of the colour and pattern of the type and the variety, would not be coterminous but would be independent.

They seem to be coterminous in cases where any attention has been paid to this point.

Lang, in his second hypothesis, has suggested that a factor can be lost in one or more somatic cells, or even in a sex cell. For instance sex factors for the female $(FG)(FG)(MA)(MA)$ might by loss of a factor become $(FG)(FG)(MA)(ma)$, i.e. those of the male. If this happened in one of the first cleavage cells, you would get a halved gynandromorph, if later a coarsely or finely mosaic-built gynandromorph. The weak point, as Poppelbaum points out, is the necessity for supposing a very large number of simultaneous mutations of the same kind in different cells in the mosaic gynandromorphs.

The existence of individuals showing a mosaic of different sex and colour, such as some of the heterochroic gynandromorphs, where each sex and colour occupies exactly the same areas, necessitates the supposition that a number of simultaneous mutations of two different and independent kinds can occur in a number of cells, but that neither mutation can occur in any cell without the other. For this to occur more than once would be miraculous, and yet it must have occurred on many occasions if Lang's hypothesis is true.

The theory in which I believe is based on the supposition that sex is a Mendelian unit character. The sex factor is probably carried by a special chromosome. Secondary sexual and sex-limited characters are

also unit characters and are probably carried by the same chromosome as the sex factor itself, whilst ordinary somatic characters are borne by the other chromosomes.

In a normal union of sperm and egg nuclei fusion of the chromatin takes place and at the subsequent cell division the nucleus of each cleavage cell receives a similar amount of chromatin of the same kind. But if the mitosis is an abnormal one or if the chromosomes of spermatozoon or ovum were themselves abnormal, the division may not be an equal one.

The first cleavage cells may receive in the one case more chromatin bearing maleness, and in the other more bearing femaleness, whilst chromatin bearing the other characters may be equally distributed. In this event an individual will be produced, in which all parts derived from the one cell will be male in character and from the other female, but that derived from either of them will be alike in somatic characters. In other words it will be a halved gynandromorph.

It is possible that this unequal division may affect only the chromatin bearing the secondary sex character producing individuals like the Hertfordshire *coridon*, and similarly the other characters borne by the chromosomes may be affected.

The following unequal divisions may take place in insects :

(1) Sex and secondary sexual characters, producing an ordinary gynandromorph. Both these are usually affected together, because probably they are carried in the same chromosome.

(2) Secondary sex character only, producing a gynandromorph like the Hertfordshire *coridon* (secondary somatic hermaphrodite).

(3) Sex and sex-limited colour character like the gynandromorphs in *Dryas*, half *paphia* male, half *valesina* female.

(4) Sex-limited colour only, producing heterochroic individuals like the *Colias*, half *edusa* female, half *helice* female.

(5) A simple somatic character, producing heterochroic insects.

(6) Sex and a simple somatic character, producing heterochroic gynandromorphs.

Of course all these phenomena could be explained equally well by Lang's first hypothesis or by Doncaster's, but they would not explain the case of homogeneous twins, one colour-blind and one with normal sight. These must have arisen from the union of a single spermatozoon with a single ovum, otherwise they would not have been identical in

every respect except that of colour-blindness. The proof that they were identical is incontrovertible.

The gynandromorphous hybrids *hybridus* and *operosa* can be explained equally well on either Goldschmidt's hypothesis or by the one just put forward. But if Goldschmidt's is the more likely for the ordinary fine mosaic hybrids, the other must be invoked to explain the very rare completely halved gynandromorphous hybrids *A. populi × ocellatus*, and for the other instances of halved hybrid gynandromorphs. In this connexion it is noteworthy that no fine mosaic gynandromorphs occur in the heterochroic group or those containing a sex-limited colour. This does suggest that fine mosaic gynandromorphs are really different and arise by a mutation, produced according to Goldschmidt by inbreeding, or like other mutations arising in a manner not yet understood. After the sudden change in the sex factors has arisen in this way, it may be propagated on Mendelian lines or die out, owing to coincident loss of sexual instinct.

Familial and hereditary cases can be explained as due to the inheritance of some abnormality of the chromosomes. Doncaster has found that the females of a race of *Abraxas grossulariata*, which produces nearly all females, have a chromosome fewer than the normal females and even than the females of the same race, which produce normal families. The occurrence of a race of *Agriades coridon*, which produces a similar excess of females and a number of gynandromorphs all of a special predominantly female type, suggests that there is some chromosome defect in this isolated colony.

There is some evidence to show that a race of gynandromorphs in which the condition is familial or hereditary tends to produce gynandromorphs of the same type, as can be seen by referring to the details already given.

The imperfect nature of the halving and the remarkable mosaic arrangement, which so markedly differentiates many insect gynandromorphs from the gynandromorphous birds and some gynandromorphous crustacea, is explained by Wheeler. In birds each of the first two cleavage cells gives rise to one half of the body and so we get a perfectly halved bird, with sex organs and somatic characters entirely male on one side and female on the other. In insects according to this author there is a syncytial arrangement of the ovum in the cleavage and preblastodermic stages, which allows of a considerable degree of nuclear migration. Hence we get nuclei with different chromatin content arranged in almost any imaginable way, and when migration has finally

ceased the groups of cells formed by subsequent divisions will lead to the mosaic arrangement of sex glands, secondary sexual apparatus, and somatic structures, which I have already referred to and laid such stress upon. Naturally nuclear migration is usually slight and so most insect gynandromorphs approximate to the halved condition. The weak point of this theory is that nuclear migration has not been observed to occur and its possibility is denied by some; but it explains better than any other how in heterochroic gynandromorphs the areas occupied by the two colours and two sexes are identical.

The fourth theory which has been advanced to explain the somatic peculiarities of unisexual gynandromorphs is that they are due to trophic changes in post-embryonic (larval and pupal) life. This has been suggested by Wittenhagen and Menzel.

In the light of our present knowledge the alteration produced must be one in the chromatin of the cells. It does not seem improbable that such changes may be produced, but since all the cells are equally affected the change must be a uniform one. It cannot explain the case of the Hertfordshire *coridon*, where the alteration is almost invariably confined to one side of the insect. In any case it only explains some instances of gynandromorphism, the symmetrical unisexual ones, which form a very small minority of those described.

It seems, however, to afford a very good explanation for the symmetrical changes produced by heat in the female of *Rhodocera rhamni*, *Saturnia caecigena*, and *Lymantria dispar*, and by the presence of Stylops in the female of *Andrena labialis* and *A. chrysosceles*.

The change produced in the male *Andrena* is merely due to imperfect development of a character present in every male, and not to the acquisition of a female character. It is not comparable to the change produced in the female *Andrena*.

The acquisition of male characters by females of these insects, and the non-acquisition of female characters by the males, are explained by the fact that the females are heterozygous for sex, the males homozygous.

Conclusions.

1. Gynandromorphs probably fall into three groups. The first two groups contain a majority of symmetrical gynandromorphs showing a blending or fine mosaic of male and female characters, and some showing characters predominantly male or female, but having on the wing streaks with the colour and pattern of the opposite sex.

These are unisexual or have sex glands containing mingled ovarian and testicular tissue.

The third group contains the completely and almost completely halved gynandromorphs, some with a coarse mosaic arrangement and some with a fine mosaic arrangement of sexual characters.

2. The first group is due to a difference in the potency of the factors for sex, or secondary sex characters, or both, occurring in the two parents. The characters behave as simple Mendelian dominants and recessives, respectively. This difference occurs in *Lymantria dispar*, and its var. *japonica*.

3. The second group is probably due to a failure in the normal process of fusion of the sex chromosomes of the spermatozoon and ovum. This is especially liable to occur in the cases where the parents are of different species.

4. In the third group the condition is due to an irregular distribution of the chromatin, which carries the factors for sex and for secondary sexual characters or for one of these alone, to the first two cleavage cells. Thus it occurs at a late stage in mitosis and not at an early stage as in the first two groups, and the first two cleavage cells are different instead of being alike in their chromatin.

5. A similar irregular distribution of the chromatin carrying a somatic character may take place, and this leads to heterochroism.

6. An irregular distribution of both sex and somatic factors may occur together and this leads to the production of a heterochroic gynandromorph.

7. The existence of these strictly parallel groups of heterochroic insects, simple gynandromorphs, and heterochroic gynandromorphs supports the view that sex is a Mendelian unit character comparable in every way to a somatic character.

8. All the genital and somatic peculiarities of the second group of gynandromorphs are due to a mosaic arrangement of groups of cells

with nuclei of different chromosome content. This was due to a similar arrangement of the embryonic cells from which the different parts developed.

9. This arrangement of the embryonic cells is made possible by the syncytial nature of the ovum in its cleavage and preblastodermic stage, which allows nuclear migration to take place to any extent. In most cases little or no migration takes place, in others it is extreme.

10. The fact that nuclear migration is usually slight accounts for the fact that gynandromorphs approaching the halved condition are much commoner than those examples which show a more or less fine mosaic of male and female characters on both sides.

11. In birds four halved gynandromorphs and one almost perfectly halved are known. This is due to the fact that from each cell produced by the first cleavage one lateral half of the individual develops. Nuclear migration is absent or very slight.

12. In insects trophic changes, heat and parasitism for example, may alter the chromosome constitution of the cells in a postembryonic stage of development, and lead to the assumption of male secondary sexual characters in a female.

This phenomenon is quite different from the kind of gynandromorphism discussed in this paper.

DESCRIPTION OF PLATES.

PLATE XXI.

Fig. 1. Heterochroic gynandromorph. *Hemerophila abruptaria*. Right ♂, ab. *brunneata* Tntt; Left ♀ type. Pair of ab. *brunneata* and of typical specimens to show that the colour segregation is not a sexual one.

Fig. 2. Heterochroic *Abraxas grossulariata* ♀. Right side type. Left side ab. *nigra*.

Figs. 3 and 4. Gynandromorphism with segregation of type colour and aberrational colour limited to female sex. *Melanargia galathea*. Mixture of type ♂ with ♀ ab. *lugens*. Note that as is the rule upper and under sides do not correspond.

Fig. 5. Three gynandromorphous *Amorpha populi* of Newman's strain (?heredity by indirect descent). For diagrams of dissections see pp. 98, 99 and 100. (*a*) Predominantly ♂. (*b*) Predominantly ♀. (*c*) Predominantly ♀.

Fig. 6. Gynandromorphous *Agriades coridon* (Herts. race). Heredity, ?by direct descent. Dissected it proved to be a secondary somatic hermaphrodite

Fig. 6*a*. Heterochroic gynandromorph. *Abraxas sylvata*. Left side ♀ type. Right side ♂ ab. *pantarioides*.

ig. 14.

ig. 15.
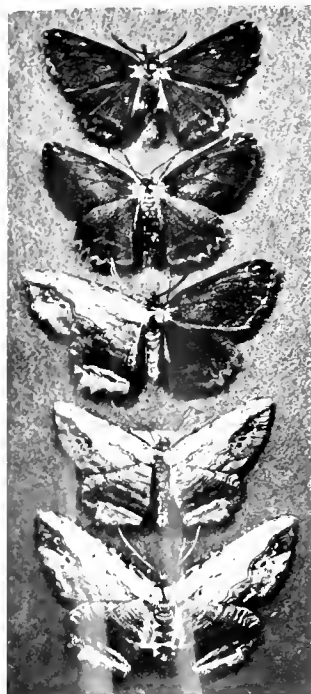
Fig. 16.

PLATE XXI

Fig. 1.

Fig. 5.

Fig. 3.

Fig. 4.

Fig. 6.

Fig. 2.
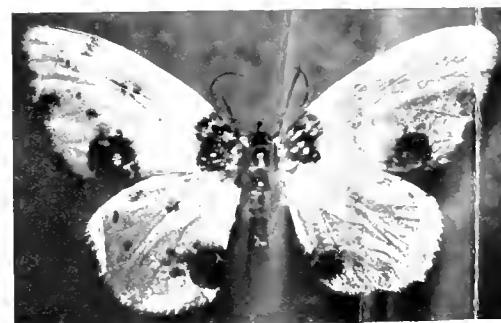
Fig. 6 a.

Fig. 14.

Fig. 15.

Fig. 16.

PLATE XXII

Fig. 7.

Fig. 12.

Fig. 13.

Fig. 8.

Figs. 10 and 11.

Fig. 12a.

Fig. 9.
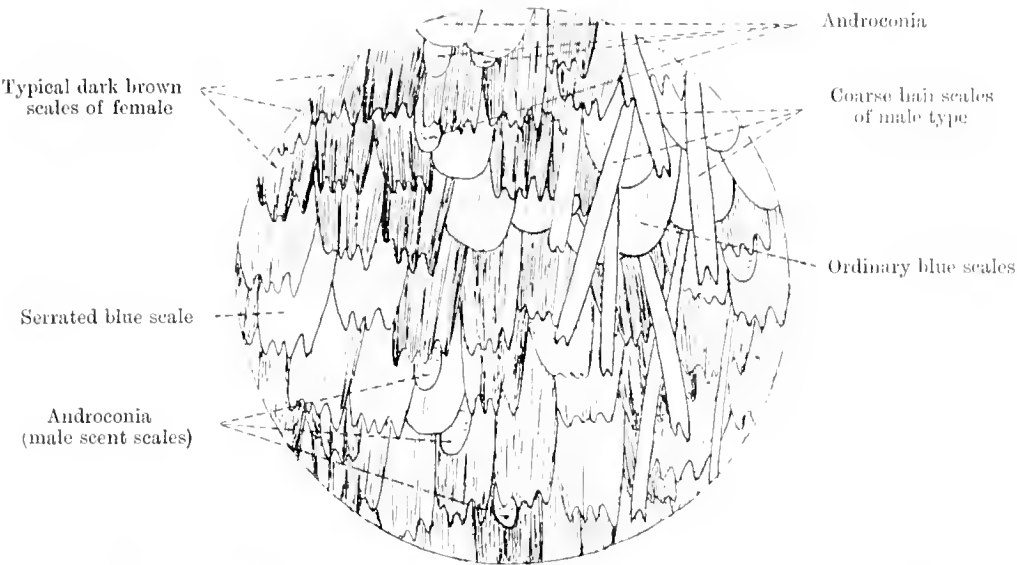
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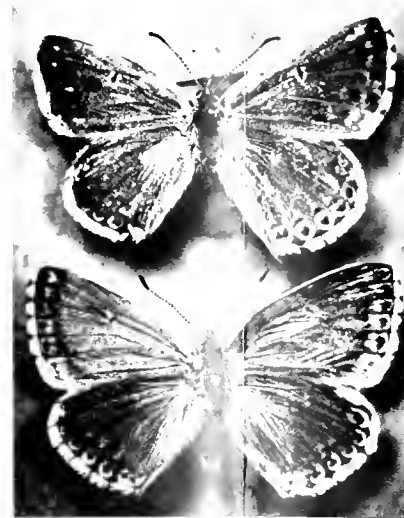
Fig. 12b.

Fig. 14.

Fig. 15

Fig. 16.

Androconia

Typical dark brown
scales of female

Coarse hair scales
of male type

Ordinary blue scales

Serrated blue scale

Androconia
(male scent scales)

Fig. 17.

Figs. 18 and 19.

PLATE XXII.

Fig. 7. Gynandromorphous *Agriades coridon* (Herts. race). Taken by the Rev. G. H. Raynor. External genitalia purely ♀. Ovaries present.

Fig. 8. Gynandromorphous *Agriades coridon* (Herts. race). Blue ♀ with male scent scales (androconia) on *both* forewings. Unique example in Mr Pickett's possession.

Fig. 9. Gynandromorphous *Agriades coridon* (Herts. race). Brown ♀ with male blue scales, hair scales and androconia on *both* forewings. External genitalia purely ♀. Ovaries present.

Figs. 10 and 11. Gynandromorphous *Agriades coridon* (Herts. race).

Fig. 10. Upper specimen has male blue scales, hair scales and androconia near central spot on right forewing, left side very small, no androconia, no blue scales. Lower *one* blue scale on left forewing, none on right. For underside see Fig. 12.

Fig. 11. Heterochroic. Right ab. *aurantia* Tutt; Left type.

Fig. 12. Underside of same insect. Note large right side ab. *parisiensis* Gerh., with black basal area, small left side with typical spotting. Great asymmetry of marginal orange lunules and of all spots. Pickett's specimen.

Figs. 12 *a* and 12 *b*. Example of gynandromorph with very asymmetrical underside. *Agriades coridon* of the Herts. race. Upper and underside. The latter shows right side small and typical; left side large and ab. *parisiensis* Gerh. The right upper side shows blue scales, androconia and male hair scales.

Fig. 13. Gynandromorphous *Agriades coridon* (Herts. race). Scanty blue (male) scaling on both wings, blunting of right apex.

Fig. 14 *a*. *Agriades coridon*, ab. *semisyngrapha*; Gynandromorphous. Left side smaller. Hair scales and androconia present.

PLATE XXIII.

Figs. 14, 15, 16. Fairly average examples of the race of Herts. *coridon* which show hereditary gynandromorphism (secondary somatic hermaphrodites). Side with male blue scales, male hair scales and androconia, small orange lunules, is smaller than purely ♀ side.

PLATE XXIV.

Fig. 17. Part of wing of gynandromorphous *Agriades coridon* of Herts. race, which on dissection proved to be a secondary somatic hermaphrodite, showing androconia, male hair scales, male blue scales both serrated and smooth, and ordinary brown serrated female scales.

Figs. 18 and 19. Upper gynandromorphous *Polyommatus icarus* predominantly ♀ ab. *coerulea* with streaks of male colour in apex of right forewing and in both hindwings, note that these cut *through* the lunules.

Lower gynandromorphous *P. icarus (symmetrical)*, predominantly male, but showing fine mosaic of female scales intimately mixed with male scales and orange lunules, also a female character.

Both are unique forms of this species.

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REDUPLICATION IN MICE.

(Preliminary Communication.)

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Darbishire's (1) experiments indicated the existence of Reduplication in Mice, and this work was undertaken to verify and extend his results. Owing to the war it has been necessary to publish prematurely, as unfortunately one of us (A. D. S.) has already been killed in France. He was a man of considerable promise, and his death is a real loss to Zoology.

The reduplication occurs between the factors named by Miss Durham(2) C and E, the absence of C producing albinism, that of E (when C is present) pink eyes and a coloured but pale coat. It is thus not possible to distinguish ce (albino) and Cee (pink eyed pigmented) mice on birth; hence mice with pink eyes dying before the hair is grown cannot be distinguished, whereas CE (dark eyed) mice are at once identifiable.

8 cc and 8 Cee mice were mated. All the cc's were of composition ccEE, two of the Cee's were Ccee, the rest CCee.

The F_1 generation consisted of 96 **CE** and 6 **cc**, the **CE**'s being therefore of composition **Ce.cE**.

They were mated together and produced 111 **CE**, 116 **Cee** or **cc**. Of these latter 74 survived to grow hair and 33 were **Cee**, 41 **cc**. If the rate of mortality is equal for **Cee** and **cc**, as Darbishire's figures suggest, the original numbers were approximately 111 **CE**, 51·7 **Cee**, 64·3 **cc**.

If the gametic series of F_1 was 1 **CE** : 1 **Ce** : 1 **cE** : 1 **ce**, the expectation would be $9 : 3 : 4$, or 127·7 **CE**, 42·6 **Cee**, 56·7 **cc**. If it was 1 **CE** : 3 **Ce** : 3 **cE** : 1 **ce**, the expectation would be $33 : 15 : 16$, or 117 **CE**, 53·2 **Cee**, 56·7 **cc**, a much closer fit.

Darbishire mated his F_1 to albinos, obtaining 378 **CE**, 368 **cc**, or nearly equality. We mated F_1 to **CCee** mice, obtaining 18 **CE**, 23 pink eyed, of which the 16 survivors were all **Cee**. This ratio suggests equality.

We next mated the F_2 mice of composition **cc** (albinos) to those of composition **ee** (pink eyed pigmented). We thus discovered which albinos were **ccEE**, **ccEe**, and **ccee**, the former giving no **Cee** offspring, the latter no **CE**, and similarly the **Cee**'s were separated into **CCee** and **Ccee**. Of the albinos 11 were **ccEE**, 9 **ccEe**, 6 either **ccEE** or **ccEe**, 1 **ccEe** or **ccee**. Of the **Cee**'s 7 were **CCee**, 11 **Ccee**, 4 doubtful.

Having thus produced a number of **Ccee** mice (either F_2 or offspring of **ccEe** × **CCee**), they were mated together, and all their albino offspring were therefore **ccee**. These were mated back to the F_1. The result was 3 **CE**, 24 **Cee** or **cc**, of which 7 survivors were **cc**.

Supposing the gametic series to have been 1 **CE**, x **Ce**, y **cE**, z **ce**, we have from the above matings :—

$1 + x = y + z$, and probably $1 + y = x + z$, also $x + y + z = \frac{24}{3}$. Hence $y = x$, $z = 1$, and $2x + 1 = 8$, $\therefore x = 3\frac{1}{2}$. Assuming however that $x = 3$, the expectation from the mating $F_1 \times$ **ccee** is $1 : 7$ or $3\frac{3}{8}$ **CE**, $23\frac{5}{8}$ **Cee** and **cc**, a close enough agreement, while without reduplication we should expect $6\frac{3}{4}$, $20\frac{1}{4}$.

The experiments are being continued and extended to rats.

CONCLUSION.

Reduplication of the "repulsion" type, probably on the basis 1:3:3:1, occurs between the colour factors in mice named by Miss Durham (2) C and E, by Hagedoorn (3) A and E.

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A SUGGESTED EXPLANATION OF THE ABNOR-MALLY HIGH RECORDS OF DOUBLES QUOTED BY GROWERS OF STOCKS (*MATTHIOLA*).

By EDITH R. SAUNDERS,

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DURING the last few years I have published a considerable amount of evidence to show that the actual output of doubles among the strains of Stocks now in cultivation does not on the average exceed 56—57 per cent., and should perhaps be put somewhat lower—possibly 53—54 per cent. These figures are based on the results of large sowings carried out during many seasons[1]. In these cultures care was taken to obtain the fullest possible record from the sample sown; no young plants were discarded at any stage of the work, thus eliminating as far as possible any effect of selection, conscious or unconscious. We still however find percentages considerably higher than the above quoted occasionally in current florists' lists, these percentages being based presumably not merely on tradition but upon observation, since the statements usually refer to newly introduced strains. In a recent catalogue of an Erfurt firm of growers, for example, 80—82 per cent. of doubles is quoted for a new strain. In his treatise on the cultivation of Stocks the French grower Chaté lists some twelve double-throwing strains ten of which will, he states, if treated according to his method, yield as many as 70 or even 80 per cent. of doubles, although these same strains ordinarily give only about 50 per cent. of doubles[2].

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[1] See *Reports to the Evolution Committee of the Royal Society*, II. 1905, p. 29; III. 1906, p. 44; IV. 1908, pp. 4, 36. *Journal of Genetics*, 1911, Vol. I. No. 4, p. 303; *Journal Royal Hort. Soc.* 1913, Vol. XXXVIII. Part III. p. 469.

[2] *Culture pratique des Giroflées*, Paris, N. D. Chaté's method was to remove all the weaker branches, and to disregard the seed in the upper half of the siliqua. Such evidence as I have obtained on this point does not indicate any such localised distribution of the double-producing seed as Chaté suggests.

Though Chaté mentions that his conclusions are the result of observation, the cultivation of Stocks having been carried on in his family for more than fifty years, he adds, in the one case in which he gives the number of seeds sown, that his percentage is calculated on a sample of only 100 seeds; hence it may be that in other cases also his sowings may not have been on a large enough scale to give reliable ratios. On the other hand one is disposed to think that some further foundation must have appeared to exist both for these statements and for those made from time to time by present day florists.

I have elsewhere shown that a differentiating character which *has the appearance* of leading to an increased output of doubles is the seemingly slightly greater viability of the double-producing seeds as compared with the single[1]. But this factor will not, we may suppose, affect the present enquiry, since the percentages claimed would certainly be quoted from sowings of *fresh* seed, not of seed *which has been kept for several seasons.* How then are we to explain such high records as those quoted by growers, assuming them to be based on accurate counts? In the course of these experiments I had come to the view that a rather greater vigour or rapidity of growth characterised the doubles as compared with the singles. If this difference could be established beyond doubt it might account for the exceptional records mentioned above. An opportunity recently presented itself to test this supposition on a fairly large scale, and a preliminary statement of the results was given at the Meeting of the British Association in 1914, when I expressed my belief that herein lies the explanation of these abnormally high percentages[2]. I am now able to give in full the evidence upon which this conclusion is based which falls under two heads :

1. A comparison of results obtained in the flower-bed with those of a control experiment carried out on the same material, showing that the apparent excess output of doubles in the first case was fictitious.

2. A comparison of the number of singles and doubles recorded among the more and the less vigorous individuals respectively, showing that a proportion in excess of expectation is furnished by the more vigorous individuals, which is counterbalanced by a corresponding deficit among the less vigorous plants.

1. During the last four years I have been able to record the results obtained with a certain fine strain of Intermediate, hoary, white Stocks

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[1] *Journal of Genetics, loc. cit.* p. 362.

[2] See *Journal Royal Hort. Soc.* 1915, Vol. xl. Part iii. p. 471.

in the beds of a College garden in Cambridge. The gardener who raised the plants saved his own seed, that of any one year providing the plants for the next season but one. Each year the yield of doubles in the beds was found to be far in excess of expectation. This excess could not be accounted for on the ground of a differential mortality between the singles and doubles after planting out, for gaps in the ranks of the flowering plants were extremely few, and in one season every individual planted out was accounted for: nor on the supposition of *intentional selection to this end* on the part of the gardener who, though pleased with his success, was yet unable to account for it, his method being simply to select the best grown plants for bedding out and to discard the rest.

The numbers recorded in the beds in four successive seasons were as follows :

	Singles	Doubles
1911	28	194
1912	17	93
1913	30	180
1914	55	216

the proportion of doubles ranging from 80 to over 85 per cent., where the expectation according to results obtained with all strains hitherto investigated would be (as stated above) under 57 per cent. A control experiment carried out with the same material proved conclusively that the excess observed among the garden plants was *not* the outcome of a corresponding excessive output of doubles by this strain but must be explained in some other way. In the control experiment seed saved from the 1911 plants was sown the following year, and—an important point—an endeavour was made to bring every seedling to flower in order to obtain the fullest record possible from the sample sown. The result was entirely in accord with previous expectation, the numbers obtained being 185 singles and 224 doubles or about 55 per cent. of doubles, thus proving that this strain behaves as regards output of doubles precisely as all other strains that have so far been tested. There is, in fact, no doubt that the strain in question is a perfectly normal one and yields only the usual slight excess of double-flowered plants. At the same time it is clear that by a suitable selection of the young plants it is possible to secure a better show of doubles in the beds than is warranted by the actual output by the germ cells.

2.   In order to obtain direct proof that a successful result depends upon the selection for planting of the most vigorous seedlings the following method was pursued.   The sowing was made in the autumn, the seeds being sown, as usual, as evenly as possible in pots, and allowed to grow undisturbed until it became necessary to give the young plants more room.   They were then repotted singly and the batch from each pot sorted into two groups according to the surface character, the one group consisting of the fully hoary, the other of the partially hoary and the glabrous plants.   Each group was then numbered off in order of size, the largest being labelled 1, the next largest 2, and so on in order[1].   The repotting was carried out in February and March when the young plants were at most 3—5 inches high, long before it was possible to determine the character of the flower since the earliest plants to flower only began to show buds in the latter part of May, many not until June and July and a large number not until the following spring.   The comparison in regard to size, however carefully made, will no doubt fail to be absolutely exact, since comparison of an individual shorter and more compact with one a little taller and more slender, or of an individual having several small leaves with one having fewer larger ones is difficult to standardise.   Furthermore slight inevitable inequalities in the environment will no doubt have some effect.   But despite some possible errors in arranging the young plants in their true sequence due to these causes, the marked difference between the ratios obtained from the groups indicated by the lower and higher numbers respectively is sufficiently striking as shown in the accompanying table.   The proportion of doubles occurring in the whole number of families taken together is very near expectation, being 220 singles to 307 doubles, or about 58 per cent. of doubles, but the proportion occurring among the most vigorous plants (indicated by the lower numbers 1, 2, 3, etc.) is very considerably in excess of this ratio, this excess being counterbalanced by a corresponding deficiency among the groups comprising the less vigorous members of the different families (indicated by the higher numbers)[2].   *We may then conclude*

[1] This preliminary sorting was carried out in order to avoid any invalidation of the results from unknown inter-relations between degree of vigour and surface character or doubleness.   This precaution appearing unnecessary was not adopted in numbering the next generation, where the whole lot of plants in a pot were numbered in one series irrespective of the surface character.

[2] At what point it is first possible to detect this difference of vigour I have not attempted to determine.   For such a determination a more stringent comparison in regard to many points would be necessary.

that doubles on the whole develop more rapidly and vigorously than the singles, and that where the period of development is sufficiently prolonged, selection based on this difference can be used as a means of securing a higher proportion of doubles in the beds than corresponds with the actual output from the parent plants.

The following figures are taken from the F_2 and F_3 generations obtained from a cross between two Intermediate (East Lothian) strains, both throwing doubles and yielding the normal output. The marked difference in the proportion of doubles obtained among the more and the less vigorous individuals is apparent in whatever way the figures are marshalled for comparison. The seedlings in each culture were numbered in order of vigour as described above and the flowers recorded. The total number of singles and doubles obtained among the plants belonging to each grade of vigour is shown in Columns 1 and 2 where it is seen that the proportion of doubles occurring among plants of the highest grade of vigour (grade 1) is far in excess of expectation, being about $3D : 1S$ instead of $9D : 7S$. As we descend the scale of vigour the proportion of doubles diminishes until we reach equality or even a slight excess on the side of the singles. The figures in the two columns are compiled from the same data treated in different ways as set forth below. By either method this relation between degree of vigour and the proportion of doubles is clearly brought out. Column 1 gives the number of singles and doubles obtained in the different grades when each individual in a culture is counted as belonging to the grade corresponding to its position in its own series. According to this method the most vigorous individual in every culture is counted in grade 1, the second most vigorous in grade 2 and so on. It is obvious that on this method of plotting the results a gap will occur in the record whenever an individual dies before flowering. The result will be a certain discrepancy in some or all of the grades between the number of singles and doubles taken together, and the number of seedlings originally classed in that grade. Column 2 gives the figures obtained when the records are plotted so that these gaps are closed up. Since such mortality as occurs may be taken to be purely haphazard we may disregard those members in a series which die young and renumber the surviving members so that they stand in the same order as before but in consecutive positions. We may illustrate this point by the following case. In a culture of 9 seedlings in which those numbered 6 and 8 die before flowering the individuals numbered 7 and 9 might either be counted as still belonging to grades 7 and 9 (the method adopted in

Analysis showing the distribution of the doubles when the plants are classified according to vigour, the sister seedlings in each pot culture being numbered (1, 2, 3, etc.) in order of vigour. The figures show a marked decrease in the proportion of doubles as we descend the scale of rigour, the number being considerably in excess of expectation in the higher grades, and deficient in the lower grades. The total for all grades together is in close agreement with expectation.

Total number of plants recorded (F_3)	307 doubles	220 singles
Expectation on the basis of a ratio of $9D : 7S$	296 ,,	231 ,,

Grade of vigour.

Columns 3 and 4.

Grade 1 includes the most vigorous individual from each series, grade 2 the next most vigorous and so on in descending order	Column 1.		Column 2.		Compiled from cultures numbered as in Column 1		Compiled from same cultures numbered as in Column 2	
	Doubles	Singles	Doubles	Singles	Doubles	Singles	Doubles	Singles
half-hoary plants								
Grade 1	46	14	54	18				
2	26	21	38	25				
3	33	13	32	21				
4	24	15	26	20				
5	25	14	22	20	Total from the more vigorous groups			
6	15	23	18	18				
7	18	17	13	11	$170\frac{1}{2}$	96	$171\frac{1}{2}$	92
8	10	10	11	7				
9	6	8	4	8				
10	8	5	4	4				
11	5	6	1	1				
12	3	3	1	1				
13	2	3	-					
14	2	—	—					
15	1	1	—					
16	—	1	.					
quarter-hoary[1] and glabrous plants					Total from the less vigorous groups			
Grade 1	31	21	32	23				
2	19	16	22	15	$136\frac{1}{2}$	124	$135\frac{1}{2}$	128
3	14	9	16	10				
4	9	8	8	10				
5	6	8	5	6				
6	1	3	—	1				
7	1	1	—	1				
8	2	—	—	—				
Totals	307	220	307	220	307	220	307	220

[1] A full account of the appearance and behaviour as regards surface character of this form, which is new, will be given in the next issue of this Journal.

[2] Where the series to be halved was composed of an odd number of individuals the middle individual was counted as half in both groups.

Column 1); or, since only 5 individuals eventually stood above them in the series, they might be counted as belonging to grades 6 and 7 (the method adopted in Column 2). We can also make the comparison in yet another way. A dividing line may be drawn half-way down in each series and the whole total made up of all the more vigorous individuals (those above the line) compared with the total from the less vigorous grades (those below the line), as shown in Columns 3 and 4. By this last-named method errors of judgment in grading are reduced to a minimum.

The results in the F_3 generation exhibit this same connexion between vigour and preponderance of doubles seen in F_2. In this case a considerable number of individuals yet remain to flower and this fact no doubt accounts for too large an excess of doubles in the total as it now stands. When the final totals are available, however, we may expect the usual approximation to the ratio $9 D : 7 S$, but no very great levelling up between the excess and deficiency seen in the higher and lower grades respectively, since it is chiefly the less vigorous, and we may suppose single individuals, which remain to be added and which will fall into the lower grades.

Analysis compiled from those plants of the F_3 generation which have flowered up to date.

						Grades									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Totals
Doubles	64	19	30	38	25	14	13	9	7	3	1	2	1	1	257
Singles	19	25	21	11	16	14	11	10	6	5	5	5	1	1	150

The plants here as in F_2 were mixed half-hoary, quarter-hoary and glabrous, being derived from quarter-hoary parents, but in this case the numbering was made irrespective of surface character[1].

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[1] See note to preceding Table.

CONTENTS

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ON THE RELATION OF HALF-HOARINESS IN MATTHIOLA TO GLABROUSNESS AND FULL HOARINESS.

By EDITH R. SAUNDERS,

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THE half-hoary Stock is not a type which one ordinarily meets with in cultivation for the reason, perhaps, that it is not listed in seedsmen's catalogues. On this account it is somewhat difficult to procure, and one's stock once allowed to run out is not easily replenished. For this form is a perfectly distinct type, and though intermediate in character between the fully hoary and the glabrous condition it cannot be obtained by the simple process of mating these forms together[1]. It is possible that it is this form which is intended by Linnaeus[2], when he speaks of "*varietas alba nuda cirque tomentosa*," but as regards its origin we have, so far as I am aware, no information.

As is common knowledge the ordinary *fully* hoary Stock is everywhere densely covered with a tomentum of characteristically branched hairs: the vegetative axes, leaves, peduncles, pedicels, sepals and siliquae all exhibit a grey-white appearance due to the presence of these hairs. Further, in double-flowered plants there may even be a sprinkling of hairs on the outer surface of the petals. I have elsewhere pointed out that such a double flower as the Stock does not differ greatly from such a vegetative shoot as the Brussels Sprout. The persistence in the double Stock flower of the terminal growing point, the presence of numerous axillary buds among the petals and the occasional development within the flower of an internode of appreciable length (as much as a quarter to half an inch) show that here the flower

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[1] Not, at least, such commercial forms as are at present available.

[2] *Species Plantarum*, 2nd ed. p. 925. 1762. There is no mention of this variety in the earlier edition (Holmiae, 1753).

shoot is far less profoundly modified than is the case with the single. In the presence of corolline hairs, which are not found in the single, even when hoary, we see the retention of yet another vegetative character.

The half-hoary type as well as the fully hoary was employed in the earliest stages of these investigations[1]. The strain then used was an annual white-flowered form which had been obtained together with some true *incana* from the Isle of Wight. It was ascertained that this half-hoary strain bred true and exhibited certain definite relations to the glabrous forms with which it was crossed. Unfortunately before these experiments were complete the half-hoary form was lost, and further investigation was held up for several years until a new half-hoary strain with pale purple (azure of commerce) flowers was by chance obtained. Being of slower growth, rather intermediate than annual in habit, this new strain was not so well suited for experiment as the one originally employed. In respect of surface character however the two types were precisely similar.

The distinctive feature of the half-hoary type is a certain definite localised inequality in the distribution of the hairs. The under surface of the leaves, the sepals and the pods are fully hoary. On the upper surface of the leaves the number of hairs is far fewer; the effect by contrast is to give a deceptive appearance of smoothness, although in fact this surface is thinly covered all over with hairs. The stem is for the most part actually glabrous, but as we pass up the shoot a certain overflow as it were of hairs from the leaf bases may give rise to decurrent hairy streaks which may become gradually more emphasised, until, in the shorter internodes of the flowering region, the glabrous area, in an extreme case, may be limited to the opposing (axillary) faces of the main axis (peduncle) and the pedicels. The partially glabrous habit readily distinguishes this from the fully hoary type.

In order to make clear the relations of the half-hoary form to the fully hoary and the glabrous types respectively it will be advantageous to restate briefly the position as to the relation in which these two latter types stand to one another. As we conclude, from the fact that some true-breeding *white* Stocks, when crossed, give rise to *coloured* offspring, that the combination of two factors (indicated by C and R) is required to produce colour, so the fact that it is possible to obtain a hoary F_1 from two coloured *glabrous* strains, or even from two individuals of the same coloured strain, leads us to assume the existence of

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[1] See "Reports to the Evolution Committee of the Royal Society," *Report I*, p. 33.

two factors (indicated by H and K) which are necessary to produce hoariness. A further point, of special interest, is that the hoary character due to the presence together of H and K is not manifested *unless the colour factors C and R are also present*; that is to say, a plant may contain H and K, but if the flower is white (or cream) *owing to the absence of C, or R, or both*, it will not be hoary[1]. This curious interdependence between the hoary character and presence of sap colour in the flower is not confined to the ordinary garden varieties of Stocks. In *M. sinuata* one likewise meets with a hoary type and a glabrous variety (var. *oyensis*) in which loss of hoariness goes with loss of flower colour. The hoary type has pale purple flowers; in the glabrous plant the flowers are white. The two are recorded as growing associated together on the Île d'Yeu off the coast of La Vendée[2].

We may express the factorial composition of the hoary and glabrous types as follows:

(1) Hoary types will contain C, R, H and K.

(2) Coloured glabrous strains may contain CRH, CRK or only CR.

(3) White or cream glabrous strains may contain any of the following single factors or groups of factors, C, R, H, K, HK, CH, CK, CHK, RH, RK, RHK; or they may lack all.

Among glabrous types then, if *homozygous*, we shall have to consider 3 possible sap-coloured forms and 12 possible whites and creams. If interbreeding occurs giving rise to *heterozygotes* we shall expect a larger number still, as many in fact as there are combinations of these factors which do not involve the presence of all four, i.e. a total of 20 among sap-colours and 45 among the white and creams. Similarly in the hoary group, to the one homozygous form we should add 15 possible heterozygotes. The precise constitution of all these different forms has been set forth in detail in an earlier paper and need not be repeated

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[1] The combination of hoariness and absence of any sap colour does however occur. We are familiar with it in the case of the white form of *incana* and in hoary white Brompton Stocks, but in these cases the white flower does not result from the *absence* of C or R. All the four factors C, R, H and K can be shown to be present; the absence of colour here must be ascribed to some other cause of the nature of inhibition. In Bromptons and some annuals the inhibition appears to be absolute, but in *incana* a noticeable tingeing of the flowers on fading affords further proof that the colour factors are not actually wanting. Whereas then in the *glabrous* whites one or both of the necessary factors for colour are absent, in *hoary* whites they are present but non-effective. It is only to the class of deficient whites (as opposed to inhibition whites) that the statement made in Punnett's *Mendelism* (3rd ed. p. 50) holds good, viz. "that in families where coloured and white Stocks occur the whites are always glabrous."

[2] See Curtis's *Botanical Magazine*, Vol. cxxvi. Tab. 7703, 1900.

here[1]. It will suffice to emphasise the fact that mere inspection of the individual in flower will not enable us to distinguish between the different forms included in any one of the three groups. There is nothing *visibly* different in the different classes of whites and creams; and among sap-coloured plants, individuals of the *same* colour and surface character *may* belong to any class within the group, or, on the other hand, plants of *different* colours (purple, red, flesh, etc.) *may* all belong to *one* class. The only method of identification at present available is the slow and laborious one of cross breeding, which necessitates the separate testing of each individual. The commercial material from which, from time to time, a fresh start had to be made was found to give very uniform results. Matings between hoary and glabrous types constantly gave all hoary[2] in F_1 and a mixed offspring in F_2 in the ratio of $3H : 1G$. When two glabrous forms were intercrossed a hoary F_1 was sometimes obtained in cases where both parents were non-sap-coloured, and again where one was sap-coloured and one not.

[1] "Further Contribution to the Study of Hoariness in Stocks (Matthiola)." *Proc. Roy. Soc.* B. Vol. LXXXV. 1912.

[2] During the progress of these experiments I have become convinced that when the hoary parent is homozygous this result invariably obtains. In the first set of experiments set out in *Report I* (*loc. cit.*) a certain number of cases are given in which glabrous individuals were recorded among the F_1 plants from the mating glabrous ♀ × hoary ♂ which, if genuine, suggested the possible occurrence of parthenogenesis. (See *Report I*, Table II. p. 38 and Table XIV. p. 83 in which the reference numbers of the particular experiments are quoted under "aberrant cases.") That these cases are *not* genuine exceptions and are *not* to be explained as due to parthenogenesis I now feel no doubt. I believe them to be due to the omission of some precaution which later experience led me to adopt, though I am still at a loss to suggest the particular cause of the experimental error.

The same remark applies to the case of *Salvia Horminum*. In the account of the investigations of the relations of the pink and white varieties to each other and to the violet type, which appears in *Report II*, two exceptions are recorded to the dominance of pink to white, and it is there suggested that these two exceptions may be due to experimental error. This we may safely hold to have been the case, for the factor relations in the case of Salvia are of the simplest type. The pink variety owes its colour to the presence of a factor P. The violet type contains the colour factor P and in addition a factor B which turns the pink colour blue. Whites lack the colour factor P and hence B which was present in the plants employed is ineffective. This view of the presence of a single colour-producing factor upon which another factor changing the class of colour may be superposed, which therefore regards the white as lacking this same colour factor rather than as containing a distinct factor W, leads us to expect the now familiar ratio $9V : 3P : 4W$ in F_2 from $P \times W$ (i.e. $bP \times Bp$) and not, as originally suggested, $2V : 1P : 1W$. The numbers actually recorded are, as will be seen on reference to the Tables, in closer agreement with the correct interpretation. The "presence and absence" view is now so familiar that this note would hardly have been called for were it not that no actual reference to this particular case putting it in line with many others happens to have been made in the course of the later work.

In every case such matings gave a proportion of hoary and smooth in F_2 approximating to $9H : 7G$. From these results it is clear that this commercial material consisted of pure (homozygous) forms and, further, that in the glabrous strains one was dealing solely with 3-factor forms (CRH, CRK, CHK and RHK). Starting with this material however it should be possible, according to the view here taken and in the absence of any indication of further complications due to coupling by appropriate matings, to eliminate successively *all* the different factors and to obtain the several simpler forms containing only 2 factors, 1 factor, or even none. From the new forms thus obtained a new set of ratios would of course result. We may state the expectation for the various cases in general terms thus :

When a hoary plant, however produced, is heterozygous in regard to any of the four factors C, R, H, K, it will yield a mixed offspring in which hoary individuals will predominate, *or* glabrous, according as the parent is heterozygous in one or two factors only, *or* in more than two. The ratio in the several cases will be as follows :

$3H$: $1G$	if the parent is heterozygous in 1 of the 4 factors.			Excess of hoary
$9H$: $7G$	,,	,,	2 ,,	,,
$27H$: $37G$	,,	,,	3 ,,	Excess of glabrous
$81H$: $175G$	,,	,,	4 ,,	,,

In the earlier accounts of this work abundant evidence has been given of the occurrence of the ratios $3H : 1G$ and $9H : 7G$[1]. It remained to obtain similar proof that by a proper sequence of matings the simpler forms, presupposed by theory, could be obtained from the more complex : in other words to procure evidence of the actual occurrence of the ratios $27H : 37G$ and $81H : 175G$.

This has now been done. F_2 families bred from grandparents containing the required combination of factors have given excess of glabrous individuals in the expected ratios, as shown by the results given below.

A. Cases where the expectation is $27H : 37G$.

		Result obtained in F_2		Expectation in F_2	
Form of mating		Hoary	Glabrous	Hoary	Glabrous
$CRHk$	$cRhK$	37	49	36	50
$crHK$	$CRhK$	41	49	38	52
$CrhK$	$cRHK$	43	54	41	56
,,	,,	18	24	18	24
,,	,,	26	30	24	32
,,	,,	28	31	25	34
,,	,,	33	50	35	48

[1] See *Reports I, II* and *III*.

B.   Cases where the expectation is $81H : 175G$.

Form of mating		Result obtained in F_2		Expectation in F_2	
		Hoary	Glabrous	Hoary	Glabrous
$CRHk$	$crhK$	17	33	16	34
,,	,,	67	135	64	138

The agreement between expectation and the results actually obtained is sufficiently convincing. If these same F_1 crossbreds are crossed back with a glabrous type instead of being self-fertilised, another series of ratios is obtained. The F_2 ratio in these cases depends upon how many of the 4 factors have been introduced into the pedigree *more than once* in the course of the two matings. We may state the results of the various possible combinations in general terms as follows :

	Various ratios obtainable in F_2 when a hoary F_1 crossbred is bred back with a glabrous type	Conditions under which these different ratios are obtained
(1)	$1H : 1G$	if 3 out of the 4 factors be introduced more than once
(2)	$1H : 3G$	if 2 out of the 4 factors be introduced more than once
(3)	$1H : 7G$	if 1 out of the 4 factors be introduced more than once
(4)	$1H : 15G$	if none out of the 4 factors be introduced more than once
(5)	all H	if each of the 4 factors be introduced more than once

Since in the early experiments, one case excepted, only 3-factor glabrous types were available, viz. CRH, CRK, CHK, RHK, the results obtained from breedings in the form heterozygous hoary × glabrous all fall into either the first or last category given above. As, by suitable breeding, material in which the several factors have been eliminated is obtained, the ratios with the higher proportions of glabrous to hoary can be shown to occur. This has already been done in case (2). From a breeding of the form $(CK \times RHK) \times CK$ in which the F_2 expectation is $1H : 3G$, two F_1 plants yielded respectively

$$8H : 23G,$$
$$1H : 3G.$$

To obtain the two higher ratios $1H : 7G$ and $1H : 15G$ is merely a question of further elimination, identification, and suitable mating.

We may therefore regard the conclusions formulated in the earlier paper quoted above[1] *as fully established.* Stated in the briefest possible way they amount to this : *That the inter-relations of the fully hoary and the glabrous types depend upon two pairs of factors (indicated by CR and HK) which segregate in the normal way, the one pair being essential for the production of sap-colour, the other for hoariness, the latter pair*

[1] See note 1, p. 148.

being however non-effective unless combined with the former. Having brought our consideration of the inter-relations of hoary and glabrous to this point, we can now proceed to consider the relations of these types to the half-hoary form.

The characteristic features of the half-hoary form have been described above (p. 146). It may be added that this type is peculiar in that the adult appearance is not assumed from the beginning as is the case with the fully hoary and glabrous types. As a rule the first leaf after the cotyledons has only quite a few hairs on the basal and extreme apical margins. The succeeding leaves exhibit an increasing degree of hairiness until about leaf 5 when the half-hoary condition is generally reached and thenceforward maintained, except that in the axillary buds a similar grading may be repeated, one or two of the first young leaves, especially if rather stunted, being very slightly hairy, the succeeding ones typical. In this behaviour we are reminded of another Crucifer, *Biscutella laevigata*, in which hairy, intermediate and glabrous forms are found. In *Biscutella* as in *Matthiola* transition stages from a juvenile to a stable adult condition—stages which may sometimes be witnessed again in an axillary shoot—commonly occur in the inter-mediate plants, but in the case of *Biscutella* the gradation is from the partially hoary towards the glabrous condition; in the half-hoary Stock it is in the opposite direction—towards the fully hoary condition[1]. This return in the axillary shoot to a grade represented at a lower level on the main axis is curious but not uncommon in plants. It is not confined to the period of vegetative development; it may equally be observed in flowering shoots as, e.g., in *Digitalis purpurea* var. *heptandra* and in *Erodium pimpinellifolium*. In *D. heptandra* as described elsewhere[2] there is a gradual transition up the spikes from a more extreme heptandrous condition towards the normal until the end of the flowering season when the flowers often show a slight retrogression towards the abnormal condition. In the axillary shoots the starting-point is usually some intermediate stage in the series—one which has already been passed through by the main axis at the time that the axillary shoot begins to flower.

In *Erodium pimpinellifolium* the flower is commonly described as having the two postero-lateral petals distinguished from the other three

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[1] Fuller details are given in an account of observations "On a discontinuous variation occurring in *Biscutella laevigata*," *Proc. Roy. Soc.* Vol. LXII.

[2] "On Inheritance of a Mutation in the Common Foxglove (*Digitalis purpurea*)," *The New Phytologist*, Vol. x. 1911, p. 54.

by the presence of a basal area or spot of a different colour from the rest of the petal, being thus distinguished from the nearly allied *E. cicutarium* in which all five petals are alike and unspotted. If however the flowers of *E. pimpinellifolium* are recorded during a season, it will be found that occasionally the earliest flower has all five petals spotted, though I do not think I have ever observed more than one flower of this type on an axis, and even one is not very common. One or two succeeding flowers may show four petals spotted, occasionally one may follow with three spots, and then the plant settles down to the 2-spot pattern until the close of the flowering season when a downgrade series begins once more, the spots diminish in size until in the last flowers they often cannot be detected at all. The point of interest is that the earlier lateral axes also often produce at first a few flowers with more than two petals spotted, although the first flowering stem may have already passed on to the stage of producing only the 2-spot flowers. We do not as yet understand the causes operating in these cases, and a statement of the facts is all that is possible.

The inter-relations existing between the half-hoary Stock and the glabrous or fully hoary types are especially interesting as they reveal to us for the first time a difference in the relations of the two factors H and K to a third factor. Hitherto in absence of evidence to the contrary these two factors have appeared to stand in a complementary but equivalent causal relation to surface character. Results obtained from any series of matings involving the presence of H but not K could equally be obtained by using the corresponding forms containing K but not H, provided that the substitution of K for H in these operations was made throughout. Such is not the case when the half-hoary form is employed in these matings, and it is from the use of this type that we obtain the first piece of evidence that the *rôle* played by one factor of the HK pair is different from and not merely complementary to that of the other.

The results of various matings in which this type was employed are set forth below (p. 153).

The condition here designated as quarter-hoary is quite definite, and the individual exhibiting this character has a definite constitution and behaviour. As regards appearance the quarter-hoary plant is at first completely glabrous, but in the later stages of development leaves are produced with marginal hairs, or with even a few on the surface. Scattered hairs may be present on the ab-axial side of the pedicels and a fair number occur on the basal region of the sepals, although not

Results obtained in F_1 when a coloured half-hoary form was bred with fully hoary or glabrous types.

Expt.
(1) Hoary white (*incana*) (*CRHK*) $\times$ ½ hoary F_1 all hoary (10 plants)

(2) ⎰ Glabrous coloured (azure) (*CRH*) $\times$,, F_1 ,, (10 ,,)
     ⎱ Reciprocal mating with flesh (*CRH*)
        instead of azure $\times$,, F_1 ,, (1 ,,)

(3) ½ hoary $\times$ glabrous sulphur-white (*RHK*) F_1 ,, (21 ,,)

(4) ⎰ Glabrous coloured (marine) (*CRK*) $\times$ ½ hoary F_1 all ¼ hoary (56 ,,)
     ⎱ Reciprocal mating F_1 ,, (10 ,,)

(5) ⎰ Glabrous white (*CK*) $\times$,, F_1 ,, (3 ,,)
     ⎱ Reciprocal mating (7 ,,)

(6) Glabrous sulphur-white (*CK*) $\times$,, F_1 ,, (5 ,,)

Results obtained in F_2 from the matings mentioned above.

(a) *From $F_1 \times$ self*

Expt.	Parents		Hoary	Half-hoary	Quarter-hoary	Glabrous
(7)	½ hoary $\times$ glabrous flesh (*CRH*)	$F_1 = H$	19	7	1	17[1]
(8)	,, $\times$ glabrous sulphur-white (*RHK*)	$F_1 = H$	41	13	3	3[1]
(9)	Glabrous marine (*CRK*) $\times$ ½ hoary	$F_1 = \frac{1}{4}H$	—	181	$297+x$	$163+y$
(10)	,, sulphur-white (*CK*) $\times$ ½ hoary	$F_1 = \frac{1}{4}H$	—	2	4	1

(b) *From $F_1 \times$ a glabrous type*

| (11) | [½ hoary $\times$ flesh (*CRH*)] $\times$ flesh (*CRH*) | 14 | — | — | 13 |

$x + y = 70$. See reference in text.

Results obtained in F_3 from the self-fertilisation of F_2 individuals obtained in Experiment 9.

Expt. 12. 8 F_2 half-hoary individuals self-fertilised yielded only half-hoary offspring (88, 63, 27, 37, 54, 59, 45, 27, respectively, making a total of 400).

Expt. 13. 3 F_2 glabrous individuals self-fertilised yielded only glabrous offspring (17, 38, 34 respectively, making a total of 89).

Expt. 14. 9 F_2 quarter-hoary individuals yielded a mixture of the three forms as follows:

	Half-hoary	Quarter-hoary	Glabrous or quarter-hoary	Glabrous
(1)	26	41	10	20
(2)	18	29	5	15
(3)	11	13	2	4
(4)	32	38	5	27
(5)	9	34	7	13
(6)	8	14	7	3
(7)	—	2	—	1
(8)	3	3	1	7
(9)	14	24	8	4
Totals	121	$198+x$	$x = \leftarrow 45 \rightarrow = y$ $(= x+y)$	$94+y$
Expectation	$114\frac{1}{2}$	229	—	$114\frac{1}{2}$

[1] In experiments 7 and 8 such a large proportion of the seeds failed to germinate that a wider deviation from the expected numerical result than one would ordinarily anticipate may well occur. For the expectation in these cases see p. 157

always in the earliest flowers. The siliqua is distinctly hairy though less so than in the half-hoary type. The stem is glabrous in the flowering as well as in the vegetative region. The appearance of the siliqua furnishes the readiest means of recognition; doubles are consequently less rapidly identified, the leaves and sepals often requiring close examination. Exceptionally, one may meet with quarter-hoary individuals showing in some limited area or member a total absence of hairs; in one plant, e.g., the second siliqua in the raceme was quite glabrous although all the others showed the quarter-hoary condition; in another the two surfaces of one siliqua were sharply differentiated, the one component carpel being characteristically hairy, the other quite glabrous. Such 'mosaic' cases are however distinctly rare. *As regards behaviour and constitution the quarter-hoary individual is a heterozygote incapable of breeding true since it forms no gametes corresponding to the appearance of the zygote.* It is comparable with the classic case of the Blue Andalusian among fowls, and like its animal countertype yields always a proportion of one of each of the parental forms from which it is derived to two of itself, the parental types breeding true, the heterozygous form yielding again this same proportion in succeeding generations. This behaviour is clearly proved by the results recorded above in F_2 (Experiments 9 and 10) and in F_3 (Experiments 12, 13, 14). In Experiment 9 where the total obtained from the quarter-hoary F_1 was 711 the expectation based on a ratio of $1G : 2\frac{1}{4}H : 1\frac{1}{2}H$ is

> 178 glabrous,
> 356 quarter-hoary,
> 178 half-hoary.

The record actually made showed

163 undoubtedly glabrous.

70 glabrous or quarter-hoary. From these 70 plants no record was obtained from the calyx and ovary, it is therefore uncertain how many of these originally glabrous plants really belonged to the smooth class and how many should be added to the quarter-hoary.

297 quarter-hoary.

181 half-hoary.

There is little doubt that, had the 70 plants which were classified only on the early vegetative character reached the flowering stage, the agreement between the observed and the expected results would have been extremely close, as it is in Experiment 10, despite the very small number recorded. The same may be said in regard to the numbers

obtained in F_3. The mixed offspring from the quarter-hoary F_2 plants occur in such proportions that we can hardly doubt that, had the 45 individuals which died early lived to maturity, the number to be added from the doubtful column to the quarter-hoary and glabrous classes respectively would have brought the totals into close agreement with expectation. As was anticipated all the glabrous and half-hoary individuals that were tested bred true.

The above series of results forms a concordant whole and gives us a new insight into the relations of the factors determining surface character. Taken in conjunction with what we already know they are explained on the following simple scheme:—

(1) That the half-hoary type lacks H but contains K together with an additional factor (indicated by J) which reacts with K to produce a certain degree of hairiness but definitely less than that exhibited by the fully hoary type.

(2) That when the amount of the dose, if we may so express it, of J is equal to that of K, H being absent, the result is the condition termed half-hoary, as seen in the half-hoary type employed which we may write $CRJK$.

(3) That when, on the other hand, one dose of J goes with a double dose of K, H as before being absent, as we have in the matings marine (CRK) × half-hoary, white (CK) × half-hoary and sulphur-white (CK) × half-hoary (see Experiments 4, 5 and 6), the result is to dilute the effect of J and to produce the quarter-hoary condition.

(By analogy it would be natural to suppose that in the converse case where the dose of J is double that of K, i.e. in the combination $JJKk$ instead of $JjKK$, the individual would be intermediate in hairiness between the half-hoary and the fully hoary state, or three-quarter-hoary. The only mating among those given above which would produce this particular combination in F_2 is $CRJK \times CRH$ (half-hoary × glabrous flesh) which gave F_2 as shown in Experiment 7. As the expectation in this case would only be 1 three-quarter-hoary individual in 32 the fact that none were recorded among the 44 plants actually raised must not be regarded as conclusive evidence that a three-quarter-hoary form recognisably distinct from the half-hoary and the fully hoary does not exist. For the present this point must remain undecided. We may however go so far as to predict that whatever the *appearance* of individuals of the composition $CRJKCRJk$ they will in *behaviour* resemble the quarter-hoary form in that they will not breed true owing to the non-existence of a gamete corresponding to this form of zygote.)

(4)   That when the JK pair is combined with H, the colour pair CR being also present, the full degree of hoariness due to the combination $CRHK$ masks the presence of J.

Whether the combination JK produces the half-hoary condition in *all* cases when H is absent, i.e. whether J, unlike H, reacts with K quite independently of C and R, has yet to be determined. The half-hoary type used in the present experiments being azure in colour obviously contained CR. The form originally used in the earliest experiments had indeed white flowers, but the absence of colour must be attributed to inhibition not to the absence of either C or R. For this half-hoary white gave all hoary in F_1 when crossed with either CRH or RHK whites and creams. Hence we must conclude that it contained both C and R and belonged to the class of inhibition whites referred to above (p. 147). Thus in neither case can we tell whether J would have been effective if either C or R had been lacking. Until a half-hoary white has been found or made which can be shown to belong to the class of defective whites this question must be left undecided. So far such a small number of extracted half-hoary plants have been flowered in matings which could yield the required combinations that the fact that those that were recorded were all coloured leaves the point still in doubt. Where a half-hoary type is crossed with a glabrous type, whether coloured or not, which lacks both H and K, we may however venture to predict that the JK pair brought in by the one parent will be effective and that the F_1 will be all half-hoary. With a half-hoary type therefore we are not able to predict as with a fully hoary type the result in F_1 when the mating is with a glabrous type of unknown composition. The fully hoary gives *always* fully hoary in F_1 whatever the composition of the glabrous parent as regards the factors $CRHJK$. The half-hoary, whether coloured or a white of the inhibition class, gives (1) fully hoary, (2) half-hoary or (3) quarter-hoary according as the glabrous type (1) contains H either with or without J and K, (2) lacks all the three factors H, J, K, or (3) contains K but not H or J. To these three cases we may even need to add a fourth. For if the glabrous parent contain J without either H or K, it is quite probable that the F_1 will be a form (three-quarter-hoary) recognizably distinct from both the half-hoary and the fully hoary.

The results recorded above being capable of interpretation on the scheme of inter-relations between the factors as here stated, we may turn back for a moment to a consideration of the results recorded in

the earlier experiments[1]. At that time the fact that the adult condition was not assumed by the partially hoary plants in the early seedling stage, and in the case of the quarter-hoary plants not until quite late on, was not fully appreciated. Moreover the experiments were carried out on a considerable scale, and limits of space compelled one to discard large numbers of individuals in the seedling stage. It is owing to this circumstance without doubt that the quarter-hoary condition was only recorded in a single individual. For the same reason it is more than probable that in many cases a number of half-hoary plants discarded at an early stage will have been wrongly classified as glabrous. If these points are borne in mind together with the explanation offered above (see note, p. 148) of the false appearance of parthenogenesis in one or two cases, the results in which some discrepancy appears to exist between observation and expectation, based on the conclusions formulated above, all fall into line, and the whole series of earlier and later experiments taken together form a concordant whole which can be simply accounted for on the supposition of certain inter-relations between various pairs of factors as set out in the present account. For convenience of reference these earlier results are restated here together with the expectation which the later work now enables us to give for the various matings which have so far been carried out.

Expectation in the case of various matings of a half-hoary type, whether a white by inhibition or having coloured sap, with fully hoary and glabrous types.

	Mating	Expectation in F_1	Hoary	Individuals containing JJK. Appearance not yet ascertained	Half-hoary	Quarter-hoary	Glabrous
(a)	$\frac{1}{2}H \times Hoary$						
	$\frac{1}{2}H \cdot CRHK$	all H	12	—	1	2	1
(b)	$\frac{1}{2}H \times Glabrous$						
	$\frac{1}{2}H \cdot CRH$	all H	36	2	5	2	19
	$\frac{1}{2}H \cdot CRK$	all $\frac{1}{2}H$	—	—	1	2	1
	$\frac{1}{2}H \times CR$	all $\frac{1}{2}H$	—	2	5	2	7
	$\frac{1}{2}H \cdot RHK$ ⎰	all H	36	—	7	14	7
	$\frac{1}{2}H \cdot CHK$ ⎱		or 36	—	3	6	19

if J proves not to be effective in the absence of CR[2]

	Mating	Expectation in F_1	Hoary		Half-hoary	Quarter-hoary	Glabrous
	$\frac{1}{2}H \times CR$	all $\frac{1}{4}H$	—	—	1	2	1
		or —	—	—	3	6	7

if J proves not to be effective in the absence of CR[2]

[1] *Reps. Evol. Ctee.*

[2] The considerable difference in the expectation as to glabrous plants in the two cases should make it easy to decide this point when once a full count has been obtained in F_2.

Conclusion.

The results recorded here and in the earlier work form a concordant body of facts concerning surface character which the scheme of factor relations here suggested enables us to bring together into a comprehensible whole. These factor relations involve five factors—C, R, H, J, K —inter-acting as three distinct pairs.

(1)   The pair CR essential to the production of sap colour.

(2)   The pair HK producing the fully hoary condition but only effective when the CR pair is also present.

(3)   The pair JK which produces a less degree of hairiness than HK. For this reason the presence of J can only be detected in the absence of H. The effect of the combination J and K is to produce the condition known as half-hoary if the individual has the constitution $JJKK$ or $JjKk$, i.e. if the dose of the two factors is equal. If K has been brought in on both sides of the pedigree and J only on one, i.e. if the individual has the constitution $JjKK$, the result is to dilute the effect of J, and the individual exhibits the lesser degree of hairiness known as quarter-hoary. It remains to determine the appearance of the individual in the reverse case when the constitution is $JJKk$, and also to ascertain whether the effect of J is independent of C and R or whether, like H, it is only effective when the colour pair is also present.

Restatement Society.

Number of Experiment in original account			
Expt. 1 (Table I. p. 36)	½ Hoary	Glabrou	there is no reason to doubt, all the plants employed were
,, 2	,,	×	,, ozygous, both the ½ hoary and the glabrous plants must
,, 9	,,	×	,, ue to experimental error. (See note 2, p. 118.)
,, 11	,,	×	,,
,, 7	,,	`	,,
,, 60 (Table VII. p. 57)		,,	,,
,, 10 (Table I. p. 36)	½ Hoary × Glabrou		hoary condition would no doubt have been developed
			e plants had been allowed to mature.
,, 49 (Table IV. p. 50)	[½ Hoary × Glabrou		pected equality of hoary and glabrous was obtained.
,, 65 (Table VII. p. 59)	[,, `	,,	egards the three ½ hoary plants see comment on Experi-
,, 52 (Table VI. p. 55)	[,, `	,,	ts 7 and 11.
,, 70 (Table IX. p. 65)	[,, `	,,	ond with expectation.
,, 69	[,, `	,,	ercial glabrous whites have been found sometimes to be a
			cure of CK and CHK. If the white employed in the final
			ng was CHK in constitution as may quite possibly have
			the case—it was not descended from the 5a individual
			iously used—the result accords well with expectation.
			have in fact *indirect* proof that such must have been the
			, for only on this view should the result which was
			ded in a mating where a fully hoary type was sub-
			ted for the half-hoary have been obtained. (See Experi-
			t 71 in the original account.)
,, 78	[½ Hoary × Glabrou		
,, 58a (Table VI. p. 55)	[,, `	,,	rd with expectation.
,, 58c	[,, `	,,	
,, 58e	[,, `	,,	
,, 57	[½ Hoary · Glabrou		e 58 plants recorded as glabrous been allowed to mature
			e is little doubt that the expectation ¾ quarter-hoary
			½ glabrous would have been recorded. (See similar case
			xperiment 20.) The F_2 plant from which F_3 was derived
			recorded as being distinctly intermediate between the
			ary and the glabrous condition, i.e. quarter-hoary, and
			e would certainly give rise to some quarter-hoary
			ring. We may regard the total 58 as representing
			rons and ¼ hoary summed together, the ratio of the
			hoary to the sum of these two being almost exact.
,, 59 (Table VII. p. 56)	[½ Hoary · Glabrou		case a few plants were grown to the flowering stage, but
			najority were discarded as seedlings, with the result that
			ably ½H as well as ¼H were recorded as glabrous. The
			ortion of fully hoary to the other three grades taken
			her is not far out.
,, 51 (Table V. p. 52)	[½ Hoary × Glabrou		ear in mind (1) that here as in the preceding experiments
,, 66 (Table VIII. p. 62)	[,, `	,,	he ¼ hoary and a certain number of the ½ hoary will
,, 56a (Table VI. p. 55) Case 3	[,, `	,,	ubtedly have been classed as glabrous, and (2) that the
			arance of the form containing the combination JJK is
,, 54	[,, ×	,,	yet known, and even if distinguishable on inspection
			the fully hoary form is likely to have been classed with
			type, we may take these results, so far as they go, as
			g as near expectation as could be expected under the
			mstances. For whereas we have recorded a total of
			H, 107 ½H, 986G the result of classifying the JJK form
			H and the ½H with G should give 159·4H, 210 ½H, 880G.
			excess of G is no doubt made up of the missing ½H
			s which were wrongly classified.
,, 56a	Case 1	[½ Hoary · Glabrou	viation from a precise result is not greater than one
	Case 2	[,, × ,,	t well expect.
	Case 4	[,, ` ,,	mark above.
	Case 5	[,, ` ,,	rd with expectation.

It must be borne in mind that at the earlier date for investigation.

† Though individuals of this constitution no doubt e indistinguishable in appearance from one or other of these classes. For the present therefore we can only in

Restatement of earliest Experiments, carried out before 1902, and described in Report I of the Evolution Committee of the Royal Society.

Number of Experiment in original account	Form of Mating	Results recorded			Expectation based on the fuller Data now available	
		Hoary	Half Hoary	Glabrous		
Expt. 1 (Table I, p. 36)	½ Hoary · Glabrous sap-colour (CRH)	34				It, as there is no reason to doubt, all the plants employed were homozygous, both the ½ hoary and the glabrous plants must be due to experimental error. (See note 2, p. 118.)
,, 2	,, × ,, ,, ,,	16		1		
,, 9	,, ,, ,, ,, ,,	9				
,, 11	,, × ,, ,, ,,	117	①		All Hoary	
,, 7	,, ,, ,, cream (RHK)	47	①	·		
,, 60 (Table VII, p. 57)	[,, ,, ,, sap-colour (CRH)] × Glabrous cream (RHK)	248	③	①		
,, 10 (Table I, p. 36)	½ Hoary · Glabrous white (CK)	—		72	All ½ Hoary	The ½ hoary condition would no doubt have been developed if the plants had been allowed to mature.
,, 14 (Table IV, p. 50)	[½ Hoary · Glabrous sap-colour (CRH)] · ditto	430	③	137		The expected equality of hoary and glabrous was obtained. As regards the three ½ hoary plants see comment on Experiments 7 and 11.
,, 65 (Table VII, p. 59)	[,, ,, ,, ,, ,, ,,] · ditto	34		36	1H · 1G	
,, 2 (Table VI, p. 55)	[,, ,, ,, ,, ,, ,,] × Glabrous cream (RHK) × ditto when F₂ = H	262		231		
,, 70 (Table IX, p. 65)	[,, ,, ,, ,, ,, ,,] · ditto	138		138	1H · 1G in some families	In accord with expectation
,, 69	[,, ,, ,, ,, ,, ,,] × Glabrous white (CK) × ditto (?CK or CHK) when F₂ = H	97		106	1H · 1G or 1H · 3 mixed G, ½H, ½H according to the constitution of the white employed in the final mating	Commercial glabrous whites have been found sometimes to be a mixture of CK and CHK. If the white employed in the final mating was CHK in constitution as may quite possibly have been the case—it was not descended from the 5a individual previously used—the result accords well with expectation. We have in fact indirect proof that such must have been the case, for only on this view should the result which was recorded in a mating where a fully hoary type was substituted for the half-hoary have been obtained. (See Experiment 71 in the original account.)
,, 78	[½ Hoary · Glabrous sap-colour (CRH)] · Glabrous cream (RHK) · ditto when F₂ = S	—		163		
,, 78 (Table VI, p. 55)	[,, ,, ,, ,, ,, ,,] · ditto	—		583	All Glabrous	In accord with expectation
,, 78	[,, ,, ,, ,, ,, ,,] · self	—		537		
,, 78	[,, ,, ,, ,, ,, ,,] · self · self when F₂ = ½H	—		56		
,, 77	[½ Hoary · Glabrous sap-colour (CRH)] × self · self when F₂ = ½H	17		58	1 ½H · 2 ½H · 1G = 1 · 3	Had the 58 plants recorded as glabrous been allowed to mature there is little doubt that the expectation ¾ quarter-hoary and ¼ glabrous would have been recorded. (See similar case of Experiment 20.) The F₂ plant from which F₃ was derived was recorded as being distinctly intermediate between the ½ hoary and the glabrous condition, i.e. quarter-hoary, and hence would certainly give rise to some quarter-hoary offspring. We may regard the total 58 as representing glabrous and ¼ hoary summed together, the ratio of the half-hoary to the sum of these two being almost exact.
,, VI (Case VII, p. 56)	[½ Hoary · Glabrous sap-colour (CRH)] · Glabrous white (CK)	119		132	1H · 1 ½H · 1 ½H · 2G = 1 · 1	In this case a few plants were grown to the flowering stage, but the majority were discarded as seedlings, with the result that probably ½H as well as ½H were recorded as glabrous. The proportion of fully hoary to the other three grades taken together is not far out.
					H · HK · ½H · ½H · G	
,, 61 (Table V, p. 52)	[½ Hoary · Glabrous sap-colour (CRH)] · self	801	40	533	773 · 43 · 107 · 13 · 408	If we bear in mind (1) that here as in the preceding experiments all the ½ hoary and a certain number of the ½ hoary will undoubtedly have been classed as glabrous, and (2) that the appearance of the form containing the combination HK is not yet known, and even if distinguishable on inspection from the fully hoary form is likely to have been classed with that type, we may take these results, so far as they go, as being as near expectation as could be expected under the circumstances. For whereas we have recorded a total of 1591H, 107 ½H, 986G the result of classifying the HK form with H and the ½H with G should give 1594H, 210 ½H, 880G. The excess of G is no doubt made up of the missing ½H plants which were wrongly classified.
,, 66 (Table VIII, p. 62)	[,, ,, ,, ,, ,, ,,] · ,,	388	52	238	382 · 21 · 53 · 21 · 201	
,, 36 (Table VI, p. 55) Case 3	[,, ,, ,, ,, ,, ,,] · ,, · self when F₂ = H	90	7	53	84 · 5 · 14 · 5 · 44 in some families	
,, 54	[,, ,, × ,, ,, ,,] × ditto	312	8	162	271 · 15 · 38 · 15 · 143	
,, 36a	[½ Hoary · Glabrous sap-colour (CRH)] · self Case 1 · self when F₂ = H	33		14	3H · 1G in some families	The deviation from a precise result is not greater than one might well expect.
	Case 2	65	—	29		See remark above.
	Case 4 [,, × ,, ,, ,, ,,] · ,,	88	32		3H · 1 ½H in some families	In accord with expectation.
	Case 5 ,, when F₂ = ½H	—	78		all ½H	

It must be borne in mind that at the earlier date the factor relations underlying these results, which only the fuller knowledge derived from later experiments has made clear, was still matter for investigation.

Though individuals of this constitution no doubt occur we do not yet know whether they are intermediate in appearance between the ½ hoary and the fully hoary (= ¼ hoary), or whether they are indistinguishable in appearance from one or other of these causes. For the present therefore we can only indicate this form by the distinctive combination of factors—HK.

THE GENETIC BEHAVIOUR OF THE HYBRID
PRIMULA KEWENSIS, AND ITS ALLIES.

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INTRODUCTION.

THE first *Primula Kewensis* was found growing among plants of *P. floribunda*, and was thought to be an accidental hybrid of *floribunda* × *verticillata*. After a period of sterility it gave rise to a perfectly fertile form of larger size widely known as a greenhouse plant, and it is to this form that the name *P. Kewensis* is generally applied.

Inasmuch as the fertile *Kewensis*, though of hybrid origin, breeds in general true, throwing at all events no plants like *floribunda* or *verticillata*, a definite problem is thus created, and our object was to investigate this case of absence of segregation.

The fertile *Kewensis* was moreover shown by Miss Digby to be a tetraploid form having double the number of chromosomes possessed by *verticillata* or *floribunda* or the original hybrid, and we hoped also to investigate the genetics of this condition. This part of the investigation remains however incomplete, and will be the subject of a later paper.

Our experiments have consisted in breeding the various forms on a considerable scale, and in making all possible cross-fertilizations between them. As regards the results of self-fertilization, in our experience the species breed true except that *floribunda* throws a definite pale-flowered recessive, called *isabellina*. The tetraploid *Kewensis* breeds true approximately, the only evident segregation being in regard to mealiness of the foliar parts. This is a recessive condition but it appears in numerous intergrading states, the interrelations of which have not been successfully analysed.

We find the consequence of crossing between any two of the forms is that almost always the resulting offspring exactly *reproduce the maternal form, showing no paternal influence.*

In such a case the obvious suggestion is that we have to deal either with actual parthenogenesis or with the phenomenon denoted by the term monolepsis, a condition, that is to say, in which the ovules need the stimulus of fertilization for their development, though they take no genetic contribution from the pollen grains. Under most stringent tests positive evidence of true parthenogenesis has been obtained; but in view of all the facts we incline to suppose that the ovules are such that while they can occasionally develop without fertilization they more commonly develop in consequence of that stimulus.

The offspring of the tetraploid *Kewensis* both on selfing and crossing being simply a reproduction of the maternal type, no fresh recombinations can in general be made, but perhaps the most interesting part of our evidence relates to the production of a single diploid individual from *Kewensis* which, in striking contrast to the behaviour of the tetraploid, has exhibited segregation of an almost normal kind.

The plant in question was raised from the self-fertilization of a *Kewensis* which had been itself raised by fertilizing *Kewensis* with *floribunda.* Among its offspring are various new colours and combinations of characters unlike any that have appeared before in cultivation. Owing to intergradation it has not been found possible hitherto to make a quite satisfactory or complete factorial analysis of these types, though their genetic nature and properties are now fairly clear.

An interesting feature of these experiments lies in the fact that the parent species dealt with differ in respect of the floral dimorphism characteristic of the Primulaceae. Whereas *floribunda* is heterostyle, *verticillata* is monomorphic, a condition only found in about five species of Primulaceae.

The story of the origin of *P. Kewensis* is now well known to horticulturists. It appeared at Kew in 1900, among plants of *P. floribunda*, and was then thought to be a hybrid between *P. floribunda* and *P. verticillata*, and this was subsequently proved to be the case. According to the story often repeated in horticultural journals, the first hybrids obtained were sterile. The plant was described and figured in the *Gardeners' Chronicle*, 1900, pp. 130 and 195. From this drawing we presume that the anthers were in the

thrum position, a feature of some interest in the light of the future history of the plant. The hybrid was propagated vegetatively and distributed by Messrs Veitch (Pl. XXV, fig. 3). No viable seed was obtained until about the year 1905, when a single plant bore seed. The following description of this plant is given in the *Gardeners' Chronicle*, Nov. 1911, p. 378: "This plant was, as we learn from Messrs Veitch, remarkable in several ways. In the first place its main inflorescence bore pin-eyed (long styled) flowers. In the second place, though the style of the flowers was long, the stamens were in the position which they occupy in thrum-eyed flowers. In other words the flowers, though pin-eyed as judging by their styles, were thrum-eyed as far as their stamens were concerned. In the third place other inflorescences which developed on this long styled plant bore ordinary thrum-eyed flowers. *Self-pollination* of the pin-eyed flowers resulted in the production of good seed, from which have been raised all the fertile plants of *P. Kewensis* now in cultivation."

We have little personal knowledge of this form. The tetraploid type is abundant in cultivation, and on its introduction the diploid gradually disappeared. Only recently have we been able, by the help of Mr Coutts, to obtain a specimen which will be the subject of further investigation.

We have been informed by Mr Garrett and Mr Coutts of the Royal Gardens, Kew, that the fertile *Kewensis* thus obtained differed in appearance from the sterile hybrid. We will refer to these differences later, but a more important difference was discovered by Miss Digby[1]. She found that whereas *P. verticillata, P. floribunda,* and the sterile hybrid have 18 chromosomes diploid number and 9 haploid number the fertile hybrid has 36 diploid and 18 haploid, being thus in the condition now called tetraploid. Moreover Digby and Farmer have since found that the chromosomes of the tetraploid are smaller than those of the diploid form[2].

Both at Kew and at Messrs Veitch's nursery, the cross between *verticillata* and *floribunda* was repeated; experience showed that the hybrid *Kewensis* is obtained very rarely, and that in the majority of cases the offspring are so-called "maternal hybrids," *i.e.* they resemble the female parent.

Throughout this paper the term *Kewensis*, unless qualified, refers to the tetraploid form.

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[1] L. Digby, *Ann. Bot.* Vol. XXVI. No. 102, April, 1912.

[2] Farmer and Digby, *Phil. Trans. R. S.*, B. 205, p. 1.

STERILITY.

Before proceeding to a detailed description of our experiments, we must refer to the very important part played by sterility. In crossing the parent species with each other or with the hybrid *Kewensis*, viable seed has only rarely been obtained. In these crosses the ovary may fail altogether to swell, or the ovary may swell and very poor seed be obtained, some of which may germinate. On the other hand, we have often obtained apparently good seed, of which none, or only one or two seeds, have germinated. We have sometimes also got apparently good seed which has failed to germinate from *Kewensis* selfed. The method of culture has been to sow the seeds directly they are ripe, or a few weeks later. The results have been the same with both methods. There has been occasional difficulty in germinating seeds of *verticillata* and *floribunda*, but we regard these species as fully fertile, and in practice the fertility of *Kewensis* is not sensibly less. The condition of the diploid form is not accurately known.

HETEROSTYLY.

It is possible that some at least of the sterility observed is due to the fact that the parent species are respectively monomorphic and dimorphic as regards their flower structure. The two forms of flowers found in heterostyle species are usually referred to as "pin" or long styled and "thrum" or short styled respectively. The anthers in the pin form are at the base of the corolla tube: the style is long and may even protrude slightly beyond the corolla tube. In the thrum form the anthers are situated near the mouth of the corolla tube, while the style is very short and extends only a little way into the corolla tube.

In the monomorphic types such as *P. verticillata* the anthers are always near the mouth of the corolla tube, the style is long, but its length is variable, the stigma being sometimes on a level with the anthers, sometimes below the anthers, and sometimes above them.

P. floribunda exhibits heterostyly differing from the usual condition. The pin form is typical, but in the thrum form we have an arrangement resembling that found in *verticillata*. The anthers are always near the mouth of the corolla tube while the pistil is long styled. The stigma may be on a level with the anthers, or it may lie above them or below them, but we have not seen any plant with the style as short as in the normal thrum condition described above.

P. Kewensis resembles *P. verticillata* in being monomorphic.

Pollen.

Darwin was the first to show that there was a structural difference between the pollen grains of the two types in dimorphic primulas, those of the "thrum" plants having a larger diameter than those of "pin" plants.

In *P. verticillata*, where only one form exists, we have not seen differences in size between pollens. The pollen of *Kewensis* is very irregular in size, and a large number of grains are bad. Scott[1] regards *P. verticillata* as being functionally dimorphic, because he found that on self-fertilization often no seed was obtained; but when fertilized by pollen from another plant the percentage of seed was greatly increased. We have no evidence on this point as we have only self-fertilized *verticillata*.

Description of Types.

In 1911 we began a series of experiments in order to investigate and test the interesting results already obtained at Kew and elsewhere. By the kindness of the authorities at Kew, and Messrs Veitch, we were supplied with abundant material for the purpose.

P. floribunda. Pl. XXV, fig. 1. Whole plant covered with glandular jointed hairs: these are of two kinds, long many celled pointed hairs and short glandular hairs. Leaves 3—6 inches long, ovate, broadly toothed, petiole broad. Scapes numerous, 4—8 inches high, bearing superposed whorls of 3—6 flowers, subtended by an involucre of 3 or 4 bracts. Corolla golden yellow, limb flat, obcordate. Scentless. Heterostyled: in the long styled form the stigma is at the mouth of the corolla tube, and the stamens are near the base of the tube: the "thrum" form has a long style, with the stigma and the stamens at the mouth of the tube. There are slight variations in these relative positions. Pollen of "thrum" 5μ, of "pins" 4μ in diameter. Habitat Himalayas: figured *B.M.* t. 6172, vol. 39, 3rd series. Sir George Watt[2] gives a description of *P. floribunda* in its native habitat: "*P. flor.* occurs in clefts on damp rocks from Kumaon to Simla and Kashmir at altitudes from 3500—6000 ft. In its area however the altitude is gradually lowered on passing westward until in the N. Punjab it occurs almost at the level of the plains, and, what is perhaps more significant still, with

[1] J. Scott, *Journ. Linn. Soc.* Vol. viii. 1865.

[2] Sir George Watt, *J. R. H. S.*, "Report of Primula Conference," Aug. 1915, p. 196, reprinted from *J. R. H. S.*, 1904, p. 295.

the depression of altitude the plant becomes large, more robust, quite glabrous, often mealy, and the bracts foliaceous. General Sir J. M⁰Donald sent me many years ago samples of the plant from the Khyber Pass. These in my opinion break down the separation of *P. verticillata* (the Abyssinian member of this series) from *P. floribunda*." A further statement differing slightly in detail is given in *J. R. H. S.*, Nov. 1914, p. 263.

P. floribunda var. *isabellina*. This variety was brought out by Haage and Schmidt in 1897, and was described by them as having pale sulphur coloured flowers. We have not been able to obtain any further information as to its origin. It is recessive to the full yellow form, and exists both in the thrum and pin form.

P. verticillata. Pl. XXV, fig. 2. Whole plant covered with meal. On the seedlings, before meal develops, short glandular hairs can be seen, as in *Kewensis*, and may be made visible in the full grown plant by dissolving the meal in alcohol. Leaves spathulate, 6—12 in. long, with long broad petioles, acutely toothed. Scapes 9 inches high and upwards, superposed whorls subtended by 4—6 leafy bracts. Flowers pale yellow. Corolla tube 1 inch long. Sweet scented. Homostyled: the anthers at the mouth of the corolla tube, the stigma at the same level or slightly protruding. Pollen $6 \cdot 1 \mu$ in diameter, uniform in size. Habitat Abyssinia. Figured in *B. M.*, t. 6042, vol. 29, 3rd series.

P. Kewensis. Sterile diploid hybrid. Pl. XXV, fig. 3. This hybrid was described in the *Gard. Chron.* Mar. 3, 1900, p. 130. From this description we have made the following abstract: Leaves 6—8 in. long, obovate-spathulate, with a long petiole-like base, the margins wavy and dentate, slightly mealy, otherwise glabrous. Scapes numerous, 12 inches long, with from 2—4 whorls of large leafy bracts, subtending whorls of from 6—10 flowers. Corolla tube 1 inch long, faintly mealy, bright yellow. Figured in *Gard. Chron.* March 1900, p. 195. It appears from this figure that the anthers were at the mouth of the tube.

P. Kewensis. Pl. XXVIII, figs. 9 and 10. Fertile tetraploid hybrid. As above but of more robust habit, leaves broader. In the F_1 hybrids the meal is confined to the calyx and corolla tube, but in succeeding generations there is great variation in the amount of meal. *P. Kewensis* v. *farinosa,* an interesting derivative variety, first raised by Messrs Veitch, is mealy all over. Short glandular hairs are present, as in *verticillata*. Sweet scented. The anthers are in the thrum position but the style varies in length. Pollen from $6 \cdot 1 — 6 \cdot 6 \mu$. We have examined a very large number of *Kewensis* plants of our own growing, and we have also

been kindly allowed to examine stocks in various nurseries. We have never seen true heterostyly in *Kewensis*; although the styles may vary in length, the anthers are always in the thrum position. The pollens examined microscopically never show the difference in size which is so marked a feature in heterostyled primulas.

We have also examined a very large number of plants with regard to the condition of the leaf surface, and we find on careful inspection that many of the plants are really hairy. The hairs are short and sparsely scattered, sometimes visible to the naked eye, but often only to be seen with the aid of a lens.

We shall refer to this tetraploid form as *Kewensis*, and the sterile hybrid we shall refer to as diploid *Kewensis*.

EVIDENCE FROM CROSS-FERTILIZATION, AND THE QUESTION OF PARTHENOGENESIS.

We began our experiments in 1911 by crossing *verticillata* with *floribunda*, and in 1912 we also made many crosses between these species and *Kewensis*. We obtained offspring which resembled the maternal parent exactly, and which generally bred true on self-fertilization. These results were in accordance with those obtained in recent years at Kew and at Messrs Veitch's.

We then started a series of experiments in 1913 to find out if parthenogenesis actually occurs. The plants were carefully emasculated and isolated. In 1914 we repeated the experiments with additional precautions, isolating the plants in glass cages, which ensures isolation but has the disadvantage of bad ventilation. Nevertheless we obtained some positive evidence of parthenogenesis.

One of the difficulties we have had to contend with in this work has been the difference in the behaviour of the flowers of the same plant on crossing. Several flowers may be pollinated by the same male parent, one only may produce viable seed, the rest either giving seed which fails to germinate or none at all. On account of these irregularities, and of the uncertain germination of the seeds, it is impossible to lay much stress on the details; we shall therefore only consider the general course of the results.

There is some evidence that individual plants, though alike in their power of giving good seed when selfed, yet differ as regards the capacity for giving good seed on cross-fertilization. For instance, a single plant

of *floribunda* var. *isabellina* was crossed with six *Kewensis* fathers, and in four of these crosses maternal hybrids were obtained; the two other crosses failed. Two of the maternal hybrids thus obtained were crossed again with *Kewensis*, and one of them gave maternal hybrids. On the other hand there is a case in which a *Kewensis* plant was fertilized by four *verticillata* fathers, one cross only gave offspring, the rest failed.

From 91 crosses of *verticillata* × *floribunda* and reciprocal, *Kewensis* appeared only twice. In each case one plant only was obtained and both these plants were fully fertile and bred true to *Kewensis*. The chromosomes of one hybrid were counted by Miss Digby, who found the haploid number to be 18 and the diploid number 36. We have never obtained the diploid original form of *Kewensis* as a result of our crosses. We may note here that *floribunda* and *verticillata* have never reappeared from the self-fertilization of *Kewensis*.

Of 28 plants of *verticillata* used as females in crosses with *floribunda* and *Kewensis*, 7 gave maternal hybrids. Of 17 plants of *verticillata* tested for parthenogenesis, one only gave viable seed. Of *floribunda*, 39 plants were used as females in crossing, 9 gave maternal hybrids. Ten plants of *floribunda* were tested for parthenogenesis, and gave no seed. Of *Kewensis*, 34 plants were used as females for crossing, and 11 gave maternal hybrids. Twelve plants of *Kewensis* were tested for parthenogenesis; 3 gave viable seed.

Tested by the viability of the seeds there is no great difference between the results of crossing and those obtained in the trials for parthenogenesis; but judged by their appearance there is a good deal of difference. In the crosses, the seed is often described as fair or good, whereas in the parthenogenesis tests only once from a *verticillata* did we obtain any seed described as good, and once seed described as fair from *Kewensis*.

Taking into consideration that the plants were in a glass cage, and the irregularities previously mentioned, the possibility that the "maternal hybrids" are parthenogenetic in origin cannot be said to be removed. The question must for the present be left open. We are continuing the experiments this year[1].

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[1] Perhaps in favour of the view that these offspring are parthenogenetic is the fact that using the pollen of *P. Forrestii*, a species far removed from this group, maternal offspring were obtained from *verticillata*.

Evidence of segregation in *Kewensis*.

The types used, however fertilized, in general give nothing but plants resembling the seed parent. *P. floribunda, floribunda isabellina,* and *verticillata,* except in three isolated cases enumerated below, which we regard as errors, have given no offspring not identical with themselves. *P. Kewensis* moreover, though a hybrid, commonly throws nothing like the species from which it is derived. Among *Kewensis* families there may be some variation, notably in the size of the plants or in the amount of meal present, and in respect of this last character the evidence points to the occurrence of segregation. One example of variation in colour occurred, and a double form has also arisen.

We have further to record a group of seven cases in which solitary individuals of unexpected nature came from *Kewensis* seed. These may not impossibly be due to errors, but for certain reasons we are disposed to regard them as instances of segregation occurring sporadically.

But the most remarkable departure from the usual genetic behaviour of these plants was the appearance, on at least one occasion[1], of a diploid individual as the offspring of the tetraploid type, and on breeding from this individual we raised families in which segregation is habitual and probably runs a normal course.

These several statements may now be amplified.

A. Aberrant cases probably due to error.

(1) A family of *verticillata* plants was sent us from Kew, arising from *vert.* × *flor.* One of these plants on self-fertilization gave a large number of *verticillata* plants and one plant of *floribunda.*

(2) A plant of *floribunda* var. *isabellina* (extracted from a cross with a diploid plant which came from *Kewensis,* no. $\frac{15}{12}$) on self-fertilization gave 28 plants, one of which had *yellow* flowers, the rest with the pale flowers of *isabellina.* The plant with yellow flowers differed from the others in several respects. This is the only case we have met with of the *isabellina* type not breeding true.

(3) A plant of *floribunda,* long styled or pin (the recessive form), extracted from a cross with a diploid form which came from *Kewensis,* no. $\frac{15}{12}$, on selfing gave three *thrums* and four pins. This is the only case we have had of a pin plant not breeding true.

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[1] Only in one of these cases have the chromosomes been counted. In one other case, the *floribunda*-like habit of the plants in question suggest that they are diploid.

B.　Aberrant cases possibly due to segregation in *Kewensis*.

In 1912, three plants of *Kewensis* were given us by the Botanic Gardens, Cambridge, and were numbered $\frac{22}{12}$, $\frac{28}{12}$ and $\frac{41}{12}$. They were used in the following crosses:—

(1)　　　　　　　*vert.* × *Kewensis* $\frac{22}{12}$　　　　　　*Kewensis* $\frac{23}{12}$ selfed

maternal hybrids of which a plant $\frac{7}{14}$ × *Kewensis* $\frac{7.8}{14}$ a plant

One plant only, *floribunda.*

(2)　　　　　　　　　　*flor.* × *vert.* 1911

maternal hybrids of which a plant $\frac{31}{12}$ · *Kewensis* $\frac{23}{12}$

maternal hybrids of which a plant $\frac{1}{15}$ × $\frac{23}{12}$ [reciprocal cross below]

1 plant only, *verticillata.*

(3)　　　　　　　　*Kewensis* $\frac{23}{12}$ × $\frac{1}{15}$

1 plant only, *verticillata.*

Compare reciprocal above.

(4)　　　　　　*floribunda* var. *is.* × 2.*x Kewensis* (at Messrs Veitch)

maternal hybrids
Kewensis $\frac{41}{12}$　　×　　$\frac{7}{12}$ a plant

1 plant only, *floribunda* yellow.

Two other aberrant cases unconnected with the above occurred.

(5)　　　　　　　　*Kewensis* × *flor.* var. *is.* (at Messrs Veitch)

maternal hybrids
flor. var. *is.*　　×　　$\frac{49}{12}$ a plant

2 plants only of which

1 = *floribunda* yellow,

1 = *floribunda* var. *isabellina.*

(6)　　　　　　　　　　*vert.* × *Kewensis*

maternal hybrids
Kewensis　　×　　a plant

1 plant only, near *floribunda.*

(7)　A plant of *Kewensis* was tested for parthenogenesis. Very poor seed was obtained, only one germinated, giving a plant of *floribunda.*

Variation in Kewensis on self-fertilization.

As already stated, *P. Kewensis* on self-fertilization generally breeds true to type, but varies in some particulars, such as size, degree of hairiness, amount of meal, and flower colour.

Size. The variations in size are considerable, small plants occurring in the same families with large plants. The chromosomes of a small plant were counted by Miss Thomas, and were found to be 36 diploid and 18 haploid. Hence the number of chromosomes is not directly connected with the size of the plant.

Hairs. The F_1 hybrids possess short stalked glands visible with a lens, resembling those seen in *verticillata* when the meal is dissolved in alcohol. In succeeding generations occasional plants of *Kewensis* occur which have hairs on the leaves visible to the naked eye, and on microscopical examination these are seen to be glandular, the stalk much longer than in *verticillata,* but still generally not so long as the long hairs of *floribunda,* although an occasional hair may attain this length. (See p. 163, description of types.)

Mealiness. Pl. XXVIII, fig. 10. The inheritance of the different degrees of mealiness has been studied in some detail. Mealiness is not an easy character to analyse. The distribution of meal on the plant may vary, as well as the quantity, and there is further the difficulty occasioned by the fact that a plant which at the beginning of the season is only slightly mealy may become mealy all over at the end of the season. Therefore the degrees of development of this character only admit of a rough classification as follows:

(1) Meal distributed over the entire surface of the plant $= M^1$.

(2) Meal on the corolla tube, calyx and bracts, and slightly on the peduncles; or restricted to the nodes and calyx, and other intermediate forms $= M^2$.

(3) Meal only present inside calyx and on corolla tube $= M^3$. (Occasionally the meal of such plants is very slight in quantity.)

We find that M^1 throws M^1 only. One exception has been met with in a family of four plants; one of these was less mealy. This exceptional plant was not kept, and we do not know if it would have developed more meal later.

Plants classified as M^3 have sometimes thrown only M^3, but our numbers are too small to prove that M^3 can be fixed. They may throw all other forms.

The intermediate forms (M^2) are always heterozygous as far as our experience goes, and throw all forms.

Owing to the difficulty of classifying the plants, we know nothing of the number of factors involved. M^1 is evidently recessive to all the other forms.

Colour. In 1914 a new flower colour appeared in one of our *Kewensis* families, very much paler than any we had seen before. It apparently breeds true. We know nothing concerning the origin of the parent of the plant which had the new colour. But in 1915 the same colour appeared in the offspring of a cross between *Kewensis* and a plant with a complicated ancestry, no. $\frac{15}{12}$. The results obtained from this plant are peculiar, and will be the subject of a separate account.

Doubling. In Messrs Veitch's nursery a double variety has been obtained. The account of its origin is of some interest. A plant (Pl. XXVI, fig. 5) with single and double flowers appeared, the doubleness varying in degree. The double flowers were sterile, and the plant was propagated by division. By repeating the process of division, plants bearing only double flowers were obtained.

ORIGIN AND GENETIC BEHAVIOUR OF A NEW DIPLOID FORM EXHIBITING NORMAL SEGREGATION.

We now come to the most interesting case of segregation in *Kewensis*. In 1911 we received from Messrs Veitch two families of *Kewensis*.

A.   Kewensis × floribunda. F_1.   Five plants *Kewensis*.

Four of these plants were selfed; the seed of only one germinated, giving two plants, one of which died before being described. The other plant, no. $\frac{15}{12}$, differed from other *Kewensis* in having a less robust habit and long narrow ovate leaves.

B.   Kewensis × floribunda var. isabellina. F_1.   Nine plants *Kewensis*.

Seed from eight of these plants was sown; five gave no germination, one gave a large number of plants all *Kewensis*, and two gave a single plant each. One of these was ordinary *Kewensis*; the other, numbered $\frac{77}{12}$, was ordinary *Kewensis* in appearance, but behaved very differently genetically. Unfortunately the chromosomes of these plants were not counted. Their genetic behaviour will be described on p. 177.

Description of $\frac{18}{12}$.   Pl. XXVI, fig. 4.

Plant less robust and smaller than *Kewensis*, very floriferous.   Many superimposed whorls of flowers subtended by leafy bracts, erect flowering stems, about 18 inches, peduncles thin.   Leaves narrow ovate covered with glandular hairs visible to the naked eye, varying in length from 1-celled stalked glands to 6-celled hairs with glands.   Meal inside calyx and on corolla tube as in *Kewensis*, slight meal at nodes. Flowers large yellow, in size and colour as in *Kewensis*, but the petals not so imbricate, and flatter.   The anthers at the mouth of the tube and the stigma at the same level; the anthers are usually shrivelled, when pollen is produced it is small in quantity, and examined microscopically only about 40 per cent. of the grains appear good.   The average diameter of the grains is $5\cdot6\,\mu$, but there is great irregularity in size and shape.

The chromosomes of this plant were counted by Miss Digby, and found to be 18 diploid and 9 haploid in number.   In this it resembles the original hybrid obtained at Kew, and this resemblance is borne out by the marked sterility which it exhibits[1].   When used as a female, either with its own pollen or with the pollen of other forms, this plant is excessively sterile, but its pollen used on *floribunda* is quite effective.

Self-fertilization has given the following results:

1912.   7 flowers selfed, gave 2 plants; 1 died before being described. $1 = \frac{24}{13}$.

1913.   Many flowers selfed, gave 1 plant $= \frac{202}{14}$.

1914.   ,,   ,,   ,,   ,,   2 plants; 1 died before being described. $1 = \frac{49}{15}$.

All the plants resulting from the self-fertilization of $\frac{18}{12}$ differ from their parent and from one another; they have characters in common with the offspring of *floribunda* $\times \frac{18}{12}$; they are smaller than the parent but vary in size, more or less hairy, never mealy, with yellow flowers. Three were thrums, and one pin.   Of these plants:

$\frac{49}{15}$ has not yet been bred from.

$\frac{24}{13}$ and $\frac{202}{14}$ were perfectly fertile and gave a large number of plants varying much, and with characters in common with the offspring of *floribunda* $\times \frac{18}{12}$.   Those characters which exhibit a wide range of variation, such as size, leaf shape, degree of hairiness, and sterility, evidently depend on a large number of factors which makes them extremely

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[1] This plant was shown to Mr Coutts and Mr Garrett of Kew, who said that it resembled the sterile hybrid *Kewensis* first obtained at Kew.

difficult to analyse. No plant like $\frac{18}{12}$ appeared. These results are in accordance with those obtained from *floribunda* $\times \frac{18}{12}$, to which we shall now pass.

P. floribunda $\times \frac{18}{12}$.

We obtained five families from this cross. In four of these crosses the *floribunda* mothers used were from the cross *floribunda* $\times$ *verticillata*, and in the fifth cross a pure-bred *floribunda* was used. There was a general resemblance between the offspring of all these crosses.

The F_1 plants showed great variation, but all of them would be classed as *floribunda*-like plants. Characters which they all possess, and which are common to *floribunda*, are the small size, dimorphic flowers, hairiness, and absence of meal. In F_2 and F_3 the same general features were exhibited. The large size, the mealy character and the scented flowers of $\frac{18}{12}$, which may be supposed to come from *verticillata*, never reappeared in these families. The difficulty of classifying all the degrees of variation which occur for every character makes it impossible for us to do more than make a general statement. Evidently a very large number of factors are involved, and except in the case of colour we shall not attempt to give precise figures.

In size, habit, leaf and flower shape, and degree of hairiness, very great variation occurs. The smaller plants do not always breed true, even when derived from the larger. The habit may be flexuous or bending as in *floribunda*, or erect as in *verticillata*, but there is a wide range of intermediates, many of which are erect in the early stages of growth and flexuous later. At the time of flowering the plants may still be single-crowned rosettes, or they may have broken up into many-crowned tufts. The former plants have hitherto bred true to this character. The time of flowering and the length of the flowering period vary greatly, and there are numerous morphological differences connected with these characters. The leaves vary from long narrow ovate as in *verticillata* to broadly ovate, and may be pointed, rounded, or obovate at the tips. The length of the petiole varies also. The petals are stellate or imbricate, flat or reflexed or funnel shaped; the corolla tubes vary in length. The hairs range from very short glandular hairs approaching the *Kewensis* type of hair to long pointed hairs like those of *floribunda*.

Sterility.

The male sterility of $\frac{18}{12}$ reappears in many of the families from *floribunda* $\times \frac{18}{12}$. In these families the anthers may contain very little

pollen or occasionally no pollen. We have no evidence as to the inheritance of the female sterility which is so marked a feature of $\frac{18}{12}$. Cases in which no seed is produced could be equally well accounted for by deficiencies in the pollen.

It is a remarkable feature of this group of plants that, though $\frac{18}{12}$ gives little seed which rarely germinates, the seed of its derivatives germinates freely.

Dimorphic structure of the flowers.

The structure of the flowers of $\frac{15}{12}$ is like that of a thrum *floribunda*, in that the anthers are at the top of the corolla tube and the style is long, the stigma protruding beyond the anthers. The plant is heterozygous, giving thrums and pins on selfing and also on crossing with a *floribunda* which is heterozygous for these characters. Among the offspring of $\frac{15}{12}$ thrums and pins occur, but within these two forms are numerous minor variations affecting the position of the anthers and the length of the style. We have sometimes had difficulty in deciding whether a plant was thrum or pin by its appearance, for plants occur in which the anthers are only half-way up the tube and the style long. On breeding from these intermediate forms we have generally found that they were capable of throwing some pins with the anthers at the base of the tube, and we have therefore accepted them as thrums. Microscopical examination of the pollen gives little help in deciding whether a plant is thrum or pin, for the grains are very irregular in size and shape and many of them are bad. The pollen of pins is generally smaller than that of thrums, but in some pins grains as large as those of thrums occur.

We have found that the pins breed true except in one case which we regard as due to an error (p. 167): the thrums breed true or throw both forms. The ratio of thrums to pins varies somewhat in different families, but there seems little reason to suppose that the two forms are not members of a simple allelomorphic pair. The irregular numbers obtained are perhaps due to the sterility which exists in varying degrees in all the families derived from $\frac{15}{12}$ and its crosses.

Flower colour. The two flower colours yellow and isabellina occur in various shades. Besides these, a new yellow colour has appeared which we have called lemon. It is very near the pale yellow of certain strains of *verticillata* but as a rule differs from these in that the margins of the petals are darker. Before giving the more complicated experiments in which the lemon colour is involved, we will consider our

records of the inheritance of yellow and isabellina (taken from various families and not confined to the descendants of $\frac{18}{12}$).

From heterozygous yellow plants selfed the total numbers are *yellow* 518 : *isabellina* 208. From heterozygous yellow × isabellina and the reciprocal cross, the total numbers are *yellow* 142 : *isabellina* 159.

The numbers from which these totals are compiled are irregular. Among 36 yellow plants selfed, the proportion of yellow : isabellina varies from 10 yellow : 14 isabellina to 13 yellow : 1 isabellina. We have not observed any relationship between the colour factor and the factor for heterostyly. In those families derived from plants heterozygous for yellow and thrum, the total numbers are :

> Yellow thrum 135 : yellow pin 33.
> Isabellina „ 32 : isabellina „ 17.

In spite of the irregular numbers, there seems no reason to doubt that yellow and isabellina are a simple allelomorphic pair.

The results of all the crosses with $\frac{18}{12}$ will now be given.

$$\frac{31}{12} \begin{bmatrix} F_1 \textit{ flor.} \times \textit{vert.} \\ \text{homozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

F_1. 26 plants all yellow.

Of these 13 plants were bred from. Twelve gave yellows only ; one plant gave

> 28 yellow as in *floribunda*.
> 2 dark yellow as in $\frac{18}{12}$.
> 9 pale yellow.
> 1 lemon.

$$\frac{37}{12} \begin{bmatrix} F_1 \textit{ flor.} \times \textit{vert.} \\ \text{heterozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

F_1. 28 plants all yellow.

Of these 9 plants were bred from. Four gave yellows only. Four gave yellows and isabellina, the total numbers being 45 yellow : 18 isabellina. One ($\frac{56}{14}$) gave

> 24 yellow.
> 6 lemon.
> 7 isabellina.

$$\frac{32}{12} \begin{bmatrix} F_1 \textit{ flor.} \times \textit{vert.} \\ \text{heterozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

$F_1 = 5$ yellow : 2 isabellina.

Two yellow plants were bred from and gave yellows only.

Certain F_2 plants from the above crosses were bred from and gave the following results:

Lemons selfed.

$$\frac{37}{14} \text{ ex } \frac{31 \times 18}{12} \text{ gave 2 lemon, like parent.}$$

$$\frac{54}{14} \text{ ex } \frac{37 \times 18}{12} \text{ gave 26 lemon : 5 isabellina.}$$

$$\frac{55}{14} \text{ ex } \frac{37 \times 18}{12} \text{ gave 26 lemon, dark and pale shades.}$$

Yellows heterozygous for lemon and isabellina selfed.

$$\frac{53}{14} \text{ ex } \frac{37 \times 18}{12} \text{ gave 7 yellow : 9 lemon : 5 isabellina.}$$

$$\frac{52}{14} \text{ ex } \frac{37 \times 18}{12} \quad ,, \quad 9 \quad ,, \quad 5 \quad ,, \quad 6 \quad ,,$$

| | Totals | 16 | 14 | 11 |

$$\frac{51}{14} \text{ ex } \frac{37 \times 18}{12} \text{ gave 10 pale yellow and lemon (not recorded separately)}$$
and 3 isabellina.

The following crosses were made among the F_1 and F_2 plants.

$$\frac{56 \times 50}{14} \text{ Yellow } F_1 \text{ (heterozygous for lemon and isabellina)} \times \text{isabellina } F_2.$$

13 yellow : 12 lemon : 17 isabellina.

$$\frac{51 \times 55}{14} \text{ Yellow } F_2 \text{ (heterozygous for lemon and isabellina)} \times \text{lemon } F_2.$$

25 yellow : 16 lemon.

$$\frac{59 \times 50}{14} \text{ Yellow } F_2 \text{ (heterozygous for lemon)} \times \text{isabellina } F_2.$$

8 yellow : 5 lemon.

We are not at present in a position to interpret these numbers. It seems probable that two pairs of factors are involved, but our numbers

are small and irregular, and we must await the results of crossing lemon with isabellina to prove the correctness of this hypothesis.

P. Kewensis $\times \frac{18}{12}$.

Many attempts to cross $\frac{18}{12}$ with *Kewensis* have been made but these crosses have generally failed. We will now give the details of a cross of this nature which gave a single fertile plant. Unfortunately we have not been able to count the chromosomes of this plant or of its offspring. In 1915 a few hybrids of $\frac{18}{12} \times$ *Kewensis* have been obtained, and we hope to continue the investigation of these hybrids, especially with regard to the inheritance of the number of chromosomes.

All attempts to cross $\frac{18}{12}$ with *verticillata* have failed.

In 1912 *Kewensis* $\frac{65}{12}$ [F_2 ex *Kewensis* $\times$ *flor.* var. *is.*] was fertilized by $\frac{18}{12}$, and gave one plant $\frac{66}{13}$, which resembled *Kewensis* but was not very robust. This plant was self-fertilized, giving 20 plants of *Kewensis*, differing from each other only as regards size. Two of the larger plants were selfed and gave *Kewensis*, but two of the smaller plants on selfing behaved differently. One such plant gave only two very small plants with leaves not more than two inches long: both had somewhat hairy leaves and meal in the calyx. The sister plant gave 5 plants, 4 of which had also somewhat hairy leaves and meal in the calyx, but 1 had hairy leaves and *no meal*. This plant also differed from the sister plants in being pin-eyed. Hence it came near *floribunda* type. The plant $\frac{66}{13}$ [F_1 ex *Kewensis* $\times \frac{18}{12}$] was crossed back with $\frac{18}{12}$, and gave two plants, one of which was typical *Kewensis*; the other was small, with somewhat hairy leaves and meal in the calyx. On selfing this plant gave 6 plants all very near the parent plant[1]. The reciprocal cross, in which $\frac{18}{12}$ was used as a female with $\frac{66}{13}$ as male, gave one plant, near *floribunda* in type but with lemon coloured flowers.

Although these results are slight, still they give evidence that segregation occurs in the offspring of *Kewensis* $\times \frac{18}{12}$, giving plants in which meal inside the calyx is combined with a considerable degree of hairiness on other parts of the plant, and finally a single plant near *floribunda* in type.

These results (except that of the reciprocal cross on $\frac{18}{12}$) are tabulated below.

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[1] The following result obtained this year gives further evidence as to the consequences of crossing the tetraploid with the diploid form. One of the 6 plants mentioned above, derived from such an original cross, selfed gave 13 *Kewensis* (not yet in flower) and 2 *hairy* plants with *lemon* flowers, thus showing that the power of segregation is now introduced. December, 1915.

Kewensis $\frac{6.6}{1.2}$

[F₂ ex *Kewensis* × *flor.* var. *isabellina*] | [F₂ ex *Kewensis* × *flor.*]

1 plant only,
Kewensis $\frac{6.6}{1.5}$ — — — $\frac{1.5}{}$
Selfed

Kewensis, 20 plants, of which four were selfed, viz.	Kewensis M^1, 1 plant, lost	1 plant, slightly hairy, meal in calyx, small. Selfed

1 large, Kewensis	1 large, Kewensis	1 small, Kewensis	1 small, Kewensis
40 plants, Kewensis	20 plants, Kewensis	2 plants, small, hairy leaves, meal in calyx	5 plants, 4 of which are hairy with meal in calyx, 1 has *no meal*, hairy leaves

2 plants, small hairy leaves, meal in calyx	3 plants, glabrous, meal in calyx	1 plant, v. slightly hairy, meal in calyx

We will now give details of another case of segregation in *Kewensis* (see p. 170).

P. Kewensis $\frac{6.6}{1.2}$ was, as already stated, typical *Kewensis* in appearance, except that the anthers were not quite at the top of the corolla tube, and the styles were shorter than is usual. There was much bad pollen. We lost the plant before we knew that there was anything exceptional in its behaviour. Self-fertilized this plant gave two plants, nos. $\frac{3}{13}$ and $\frac{19}{13}$.

$\frac{3}{13}$. Smaller plant than *Kewensis*. Leaves broadly ovate. Whole plant covered with hairs, visible to the naked eye but short and glandular. No meal. Flowers pale yellow, small, flat and imbricate. *Thrum*. Robust habit.

$\frac{19}{13}$. Small plant, flower stems only 6 inches high. Leaves narrow ovate (as in *verticillata*) but only 3 inches long. Hairs as in $\frac{3}{13}$. Flowers pale yellow, small, funnel-shaped. *Pin*.

Both these plants were selfed; the seed of $\frac{3}{13}$ failed to germinate in 1913, but selfed again in 1914 it gave

6 yellow thrum : 1 yellow pin.

3 isabellina thrum : 2 isabellina pin.

These plants varied from slightly hairy to moderately hairy.

On selfing, $\frac{19}{13}$ gave yellows and isabellina in the numbers 43 : 13. The yellows were pale in tint and there were two shades of isabellina.

All the plants were small flowered, pin, and all had a neat bushy habit with erect flower stems crowded together, the pedicels often sloping upwards instead of standing out at right angles to the main stem. Eleven of the plants had funnel-shaped flowers, and the rest flat stellate flowers. The size of these plants varied much, the internodes of one of the smallest measuring about $\frac{1}{2}$ inch, and of one of the tallest about 1 inch. It was remarkable that not one of these plants had leaves like the parent: they varied from ovate to broadly ovate.

Reciprocal crosses between $\frac{79}{13}$ and $\frac{3}{13}$ were made, and gave a total of

32 yellow thrums : 15 yellow pins.

2 isabellina thrums : 7 isabellina pins.

The results of these crosses as regards other characters are difficult to analyze : one plant only was obtained with narrow ovate leaves as in $\frac{79}{13}$. Two plants with weak stems and straggling habit appeared ; as $\frac{79}{13}$ threw only erect bushy plants we must suppose that $\frac{3}{13}$ was heterozygous as regards habit.

Two crosses were made between $\frac{3}{13}$ and *Kewensis*, both of which failed.

Recapitulation of the foregoing section.

The two plants $\frac{18}{12}$ and $\frac{77}{12}$, both of which descend from the cross *Kewensis* × *floribunda*, exhibit in their offspring and descendants a wide range of variation. These forms possess characters derived from the original parent forms *verticillata* and *floribunda*, but they bear a stronger resemblance to *floribunda* than to *verticillata* or *Kewensis*. Thus in size, absence of meal, presence of hairs, and heterostyly, are seen evidences of *floribunda* influence which are common to all the plants, whereas in habit of growth, leaf shape, flower shape, and colour, the influence of either species may be seen. The recombination of parental factors occurs also as the result of crossing *Kewensis* with $\frac{18}{12}$, when the *floribunda* type has reappeared. It appears that in $\frac{18}{12}$ we have a plant which forms a link between *floribunda* and *Kewensis*, by which characters from both forms may be recombined. The barrier that prevents the recombination of certain *verticillata* characters, such as size and habit, with the full degree of hairiness of *floribunda*, may perhaps break down in the offspring of $\frac{18}{12}$ × *Kewensis*.

P. KEWENSIS COMPARED WITH OTHER TETRAPLOIDS.

The genetics of two other tetraploid forms, viz. *Œnothera gigas*[1] and *Primula sinensis*[2], have been studied. Neither of these tetraploids arose as the result of crossing two species, and therefore they are not parallel cases with *Kewensis*, still it is of some interest to compare them.

Although these three tetraploid forms are alike in possessing double the number of chromosomes of the types from which they come, we do not know if they resemble each other as regards the comparative size of the chromosomes. As shown by Farmer and Digby[3], " the total amount of chromosome substance in the nuclei of each of the two types of hybrids known as *P. Kewensis* is the same. The nuclei of the one form of hybrid contain twice as many chromosomes as the nuclei of the other type, but the increase in number is associated with a corresponding diminution in size." Although the size of the chromosomes in the tetraploid is thus diminished, the size of the nuclei and cells are larger than in the diploid. In their discussion of these facts, Farmer and Digby conclude that the doubled number of chromosomes may be attributed to a transverse fission of the "normal" chromosomes. They suggest that the increase in size of nuclei and cells may be due to a correlation between these sizes and the superficial area of the chromosomes, for the transverse fission of the chromosomes would add to the normal amount of free surface. The volume of the chromosomes in *Œ. gigas* and in the tetraploid *P. sinensis* have not been determined, but another giant form of *P. sinensis* has been investigated by Gregory[4]. This giant was found to have the diploid number of chromosomes, but nuclei and cells larger than in the normal form.

It remains to consider to what extent the doubling in the number of chromosomes is correlated with an increase in the size of the plants. In the case of *Œ. gigas* the evidence is not perfectly consistent, the work of Geerts and Stomps, and that of Miss Lutz, giving different results. Heribert-Nilsson[5] (refs. given) concludes that the doubling of the chromosome number is not the primary cause of the peculiar habit of *gigas*. In the tetraploid form of *P. sinensis* the correlation

[1] H. de Vries, *Gruppenweise Artbildung*, 1913.

[2] R. P. Gregory, *Proc. R. S.*, B. 87, 597.

[3] Farmer and Digby, *Phil. Trans. R. S.*, B. 205.

[4] R. P. Gregory, *Proc. Camb. Phil. Soc.* Vol. xv. Part III. p. 239.

[5] N. Heribert-Nilsson, *Spaltungserscheinungen der Œnothera Lamarckiana*, 1915; Lunds Universitets Arskrift.

between size and chromosome number appears definite, but in the diploid giant there is a general increase in size without a doubling of the chromosome number. In *Kewensis* the tetraploid varies considerably in size, the small plants being no larger than the diploid form; the chromosomes of one of these small plants were counted by Miss Thomas, and were found to be 36 diploid number, 18 haploid number. It is doubtful whether the tetraploid attains a greater size than well-grown plants of *verticillata*, certainly not greater than might be accounted for by the increase of vigour often seen in hybrids. It is desirable that further chromosome counts should be made, meanwhile we must assume that number of chromosomes is not directly associated with the size of plant.

In the tetraploid *P. sinensis*, Gregory found that the factorial system is doubled, while in the diploid giant this is not so. We cannot say if the tetraploid *Kewensis* possesses a doubled factorial system, for we have no diploid form with which to compare it. The only characters which exhibit anything like normal segregation in *Kewensis* are the various degrees of mealiness, and the phenomena met with in the inheritance of these characters might be equally well accounted for by the doubling of a few pairs of factors or by the presence of several factors.

In *P. sinensis* fertilization cannot be effected between the tetraploid and diploid forms, but in *Kewensis* this is not the case.

The genetic behaviour of *Œ. gigas* exhibits certain puzzling features. Dwarf forms are thrown by it in the proportion of 40 per cent., but we are not told if these are diploid or tetraploid. A narrow-leaved form appears but de Vries considers the leaf breadth to be a fluctuating character. Crosses between *gigas* and other forms have given various results in the hands of different workers. It seems probable that individual plants differ in their genetic constitution, in spite of the fact that they breed true to *gigas* on self-fertilization. (For summary of facts and discussion see Heribert-Nilsson[1].)

SUMMARY.

I. From the cross *P. verticillata* by *floribunda* and the reciprocal, plants resembling the female parent are generally obtained. Their origin as the result of parthenogenesis cannot be held to be disproved, but these maternal hybrids rarely show any evidence of segregation when used for crossing, and usually on self-fertilization breed true to type.

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[1] N. Heribert-Nilsson. *Spaltungserscheinungen der Œnothera Lamarckiana*, 1915.

II. Occasionally hybrids of the form known as *P. Kewensis* are obtained. These are of two kinds, one partially sterile, having the diploid number 18 chromosomes, the haploid number 9 chromosomes, the other fertile and having 36 and 18 chromosomes respectively.

III. The hybrids whether maternal or otherwise are obtained in very small numbers, and although F_1 seed which appears good is often formed, great difficulty in germinating it is met with. Uncertain germination is however common in these plants.

IV. *P. Kewensis* self-fertilized generally breeds true to type, segregating only in certain factors such as degree of mealiness and flower colour; when crossed with parent types it commonly produces maternal hybrids, but in rare cases gives evidence of segregation.

V. The genetic behaviour of two plants of *Kewensis*, bred from *Kewensis* [F_1 *Kewensis* × *floribunda*], received from Messrs Veitch in 1911, was however peculiar. The offspring of these plants did not resemble *Kewensis*, but approached nearer to *floribunda*. One of them was found to have 18 diploid and 9 haploid numbers of chromosomes, and this plant exhibited segregation, giving new forms representing recombinations of *floribunda* and *verticillata* characters. These plants are also peculiar in that their seed germinates freely.

VI. Among these new forms are many shades of yellow not previously known in these plants. When we began our work, the only colours known were the full yellow of *floribunda* type and of *Kewensis*, the paler yellow of *verticillata*, and the pale cream yellow of the variety of *floribunda* known as *isabellina*. The full yellow and the pale isabellina shade evidently depend on a factorial difference, the full yellow being a dominant. The numbers given have however a wide range of irregularity. The factorial inter-relations of the new colours have not yet been sufficiently investigated.

VII. The diploid plant which thus exhibits segregation has also been crossed successfully with *Kewensis* tetraploid. From this cross plants intermediate between *floribunda* and *Kewensis* have arisen, and also a few plants resembling *floribunda*.

DESCRIPTION OF PLATES.

PLATE XXV.

Fig. 1. *Primula floribunda.*

Fig. 2. *P. verticillata.*

Fig. 3. *P. floribunda × verticillata.* The diploid F_1, first obtained at Kew. Figure kindly supplied by Sir Harry Veitch.

PLATE XXVI.

Fig. 4. The plant numbered $\frac{1}{12}$. See text.

Fig. 5. *P. Kewensis,* tetraploid, with some double flowers; seen at Messrs Veitch's.

PLATE XXVII.

Fig. 6. Leaf of *P. verticillata.*

Fig. 7. Leaf of *P. floribunda.* Note the hairs.

Fig. 8. Leaf of *P. Kewensis,* diploid.

PLATE XXVIII.

Fig. 9. Leaf of *P. Kewensis,* tetraploid.

Fig. 10. Leaf of ditto, mealy variety.

Fig. 11. Leaf of $\frac{1}{12}$.

The leaves are all shown as seen from the dorsal surface.

PLATE XXIX.

Figs. 12—16 show the series of colours which occur among the derivatives of the cross *floribunda* × $\frac{1}{12}$.

Fig. 12. Light isabellina.

Fig. 13. Isabellina.

Fig. 14. Lemon.

Fig. 15. Light yellow.

Fig. 16. Dark yellow.

Fig. 17. Diploid *Kewensis.*

The coloured drawings represented in these Plates were made by Mr Osterstock from the plants. The reproductions are fairly accurate, but in the originals the distinctions between the colour-varieties are somewhat more pronounced.

Fig. 1

Fig. 2

PLATE XXV

FIG. 3.

Fig. 1

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

PLATE XXVIII

Fig. 9.

Fig. 10.

Fig. 11.

PLATE XXIX
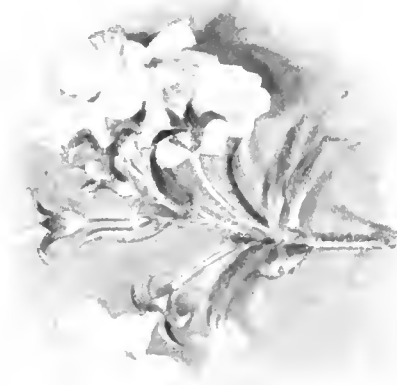
Lemon.

Fig. 14.

Isabellina.

Fig. 13.

Light isabellina.

Fig. 12.

Yellow. Diploid Æ- œ-.
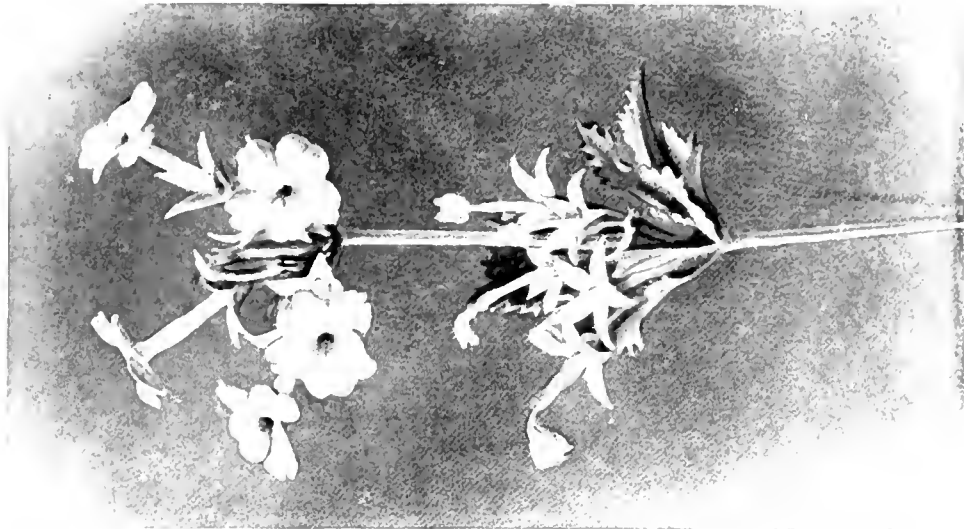
Fig. 17.
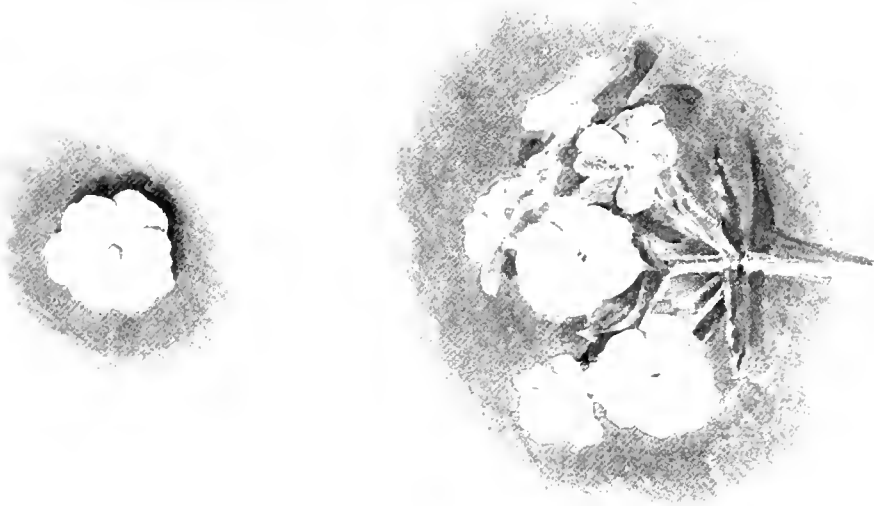
Dark Yellow.

Fig. 16.

Light Yellow.

Fig. 15.

SOME EXPERIMENTS IN HEREDITY WITH *ABRAXAS GROSSULARIATA* AND TWO OF ITS VARIETIES.

By the Rev. J. M. WOODLOCK, S.J., M.A.,

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THE experiments were carried out in conjunction with the Rev. G. Waddington, S.J., who had obtained some larvae of the var. *lacticolor* through the kindness of the Rev. G. H. Raynor of Hazeleigh Rectory, Essex, and Dr L. Doncaster. They were carried out in the intervals of other important work, which must serve to excuse their incompleteness.

The new variety of *Abraxas grossulariata* termed "Q" in this note is somewhat like *lacticolor* in appearance, though not quite so pronounced, as the black markings are sharper in outline and generally rather heavier and the distinctive cream colour of *lacticolor* is practically absent; nor has it the soft surface texture of *lacticolor*: it differs also in that the black markings other than the discoidal spots are visible on the under surface of the wings, which is not the case in *lacticolor*. It was found in the grounds of Milltown Park, Dublin.

"Q" appears to be a simple recessive to *grossulariata* as the following results show:

F_1. *Grossulariata* ♂ × "Q" ♀ gave about 50, all *grossulariata* in type.

F_2. From these six pairings were made: the resulting numbers were small, chiefly owing to heavy mortality in the egg just before hatching due to dryness, and also from the fact that, as the parents were forced out in March, the larvae were in the hibernating stage during

the heat of the summer and were not kept sufficiently damp. The numbers are: *grossulariata* ♂ 12, *grossulariata* ♀ 16, "*Q*" ♂ 8, "*Q*" ♀ 8.

A pairing was also obtained between a "*Q*" ♂ and a *grossulariata* ♀ heterozygous for "*Q*" (from *grossulariata* ♂ × "*Q*" ♀). From this resulted 6 *grossulariata* ♂, 6 *grossulariata* ♀, 5 "*Q*" ♂, 6 "*Q*" ♀.

From three families "*Q*" ♂ × "*Q*" ♀ there resulted only 13 "*Q*" (♂ and ♀), no *grossulariata*.

Included among the *grossulariata* there is another type, rather indeterminate and merging imperceptibly into *grossulariata*, but quite clear in some cases, which is distinguished by a more or less complete gap in the centre of the row of black spots outside the yellow band on the upper wing. Individuals of this type appear to be heterozygous for "*Q*" (though only a small proportion of F_1 *grossulariata* ♂ × "*Q*" ♀ were so marked, about 10 out of 50), for a pairing between two of this type—of uncertain parentage—gave *grossulariata* ♂ 17, *grossulariata* ♀ 14, "*Q*" ♂ 8, "*Q*" ♀ 11.

These experiments seem to make it certain that "*Q*" is a simple recessive to *grossulariata*. The further pairings, which were made with a view to discovering the relations between "*Q*" and *lacticolor*, were very unsatisfactory as regards quantitative results owing to various causes, the chief being ill-advised forcing which left the larvae "hibernating" during the summer of 1914 when owing to absence I could not attend to them, and the necessity of carrying them about in unsuitable boxes in 1915: qualitatively however the results were interesting.

A (i). The first pairing was made on April 5th, 1914, *lacticolor* ♂ × "*Q*" ♀. This resulted in 3 *grossulariata* ♂ and 5 *lacticolor* ♀.

(ii) Another on April 27th, 1914, between similar parents, *lacticolor* ♂ × "*Q*" ♀ gave only 3 *grossulariata* ♂.

B. April 17th, 1914, "*Q*" ♂ × *lacticolor* ♀. This pairing gave 14 ♂ and 19 ♀, all *grossulariata* in type (including some with the gap in the row of black spots outside the yellow band mentioned above).

The interest in these of course lies in the dominant resulting from a cross between two different recessives.

C. August 1st, 1914, a pairing was obtained between ♂ and ♀ of *grossulariata* type from family *B*, i.e. F_2 for both *lacticolor* and "*Q*." This resulted in:

15 *grossulariata* ♂, 3 *grossulariata* ♀, 7 "*Q*" ♂, 5 *lacticolor* ♀.

The preponderance of males is probably due to the fact that 23 out of the 30 went straight through in the autumn without hibernating, only 7 of those that hibernated finally emerging in March 1915.

D (i).   July 27th, 1914, *grossulariata* ♂ (from family *B*) × "*Q*" ♀. This gave :

4 *grossulariata* ♂, 2 *grossulariata* ♀, 3 "*Q*" ♂, 3 "*Q*" ♀, 4 *lacticolor* ♀.

(ii)   October 30th, 1914, *grossulariata* ♂ (from *A* (ii)) · "*Q*" ♀ gave only 1 *grossulariata* ♂, 1 "*Q*" ♀, 2 *lacticolor* ♀.

E.   November 10th, 1914, *grossulariata* ♂ (from family *D* (i)) × *grossulariata* ♀ (from family *B*) gave only 2 "*Q*" ♀.

At this stage the results were submitted to Dr Doncaster, who suggested that they might be explained in the same way as the production of a coloured flower by crossing two different whites in the sweet-pea, or perhaps are more nearly comparable with the production of a wild-coloured rat or rabbit by crossing an albino with a black.

It is clear that the typical *grossulariata* pattern must depend on the presence of two factors, which may be called **G** and **T**. In the absence of the factor **G** the moth is *lacticolor*, and this factor is sex-limited in inheritance, normal males being **GG**, females **Gg**.

The factor **T** is necessary for the production of the type form ; when it is absent (or if a notation be preferred which does not commit one to the presence-and-absence hypothesis, when it is modified to **Q**) the moth is of the variety "*Q*." A normal *grossulariata* male is thus **GGTT**, female **GgTT**: a "*Q*" male **GGtt** (or if preferred it may be written **GGQQ**), "*Q*" female **Ggtt**: a *lacticolor* male and female **ggTT**.

If now a "*Q*" male is mated with a *lacticolor* female, the result will be the production of typical *grossulariata* if the *lacticolor* is carrying the factor **T**, thus

$$\text{"} Q \text{"} \; ♂ = \textbf{GGtt} \times \textbf{ggTT} = lacticolor \; ♀$$

♂ **GgTt**   **GgTt** ♀,

and when the F_1 moths are mated together the result will be, in the males, typical *grossulariata* and "*Q*" in the ratio of 3 : 1, and in the females *grossulariata*, *lacticolor*, and "*Q*" in the ratio of 3 : 4 : 1, thus :

grossulariata   ♂ **GgTt**   ×   **GgTt** ♀ *grossulariata*

Spermatozoa **GT, Gt, gT, gt**   ♂ **GT,** ♂ **Gt,** ♀ **gT,** ♀ **gt** eggs.

F_2 Males **GGTT** = *grossulariata* F_2 Females   **GgTT** = *grossulariata*

2 **GGTt** = *grossulariata*   2 **GgTt** = *grossulariata*

GGtt = " Q "   **Ggtt** = " Q "

GgTT = *grossulariata*   **ggTT** = *lacticolor*

2 **GgTt** = *grossulariata*   2 **ggTt** = *lacticolor*

Ggtt = " Q "   **ggtt** = *lacticolor*

The new form **ggtt** will doubtless be *lacticolor*, since it lacks the factor **G**; it will be a *lacticolor* carrying the factor for " Q " instead of for the type form.

As will be seen from mating *C* the observed results are in fair accord with the hypothesis, and this is also the case with matings *D* (i) and (ii) and *E*.

If this hypothesis is correct, among the F_2 offspring from the cross " Q " ♂ × *lacticolor* ♀ there should be " Q " males of type **Ggtt** and *lacticolor* females of the types **ggTt** and **ggtt**, and that such types may exist is indicated by two pairings made subsequently in 1915, viz. *F* and *G*.

F. About March 10th, 1915, " Q " ♂ × *grossulariata* ♀ (both parents from family *C*). This gave only : 4 *grossulariata* ♀ and 4 *lacticolor* ♀, besides one extracted dead from the pupa which appeared to be " Q " ♀ but might possibly have been *lacticolor* ♀.

G. About the same date, *grossulariata* ♂ (from family *C* or *D* (i)) × *lacticolor* ♀ (from family *C* or *D* (ii)) gave only 3 " Q " ♀ and 3 *lacticolor* ♀.

The interest here lies in the fact that in family *F lacticolor* ♀ appears showing the constitution of the " Q " ♂ parent to have been **Ggtt**, for a *lacticolor* could not be the offspring of a normal " Q " ♂ of the type **GGtt**. Similarly in family *G* " Q " ♀ is produced showing that the *lacticolor* ♀ parent was either **ggTt** or **ggtt** (and not **ggTT**— the normal *lacticolor* constitution).

A test for the form **ggtt** would be to mate it with a normal " Q " ♂ —i.e., one which had not descended through *lacticolor*—in which case the offspring should all be " Q."

The fact that only females appear in *F* and *G* may be accidental or possibly the *lacticolor* may have been derived from Dr Doncaster's
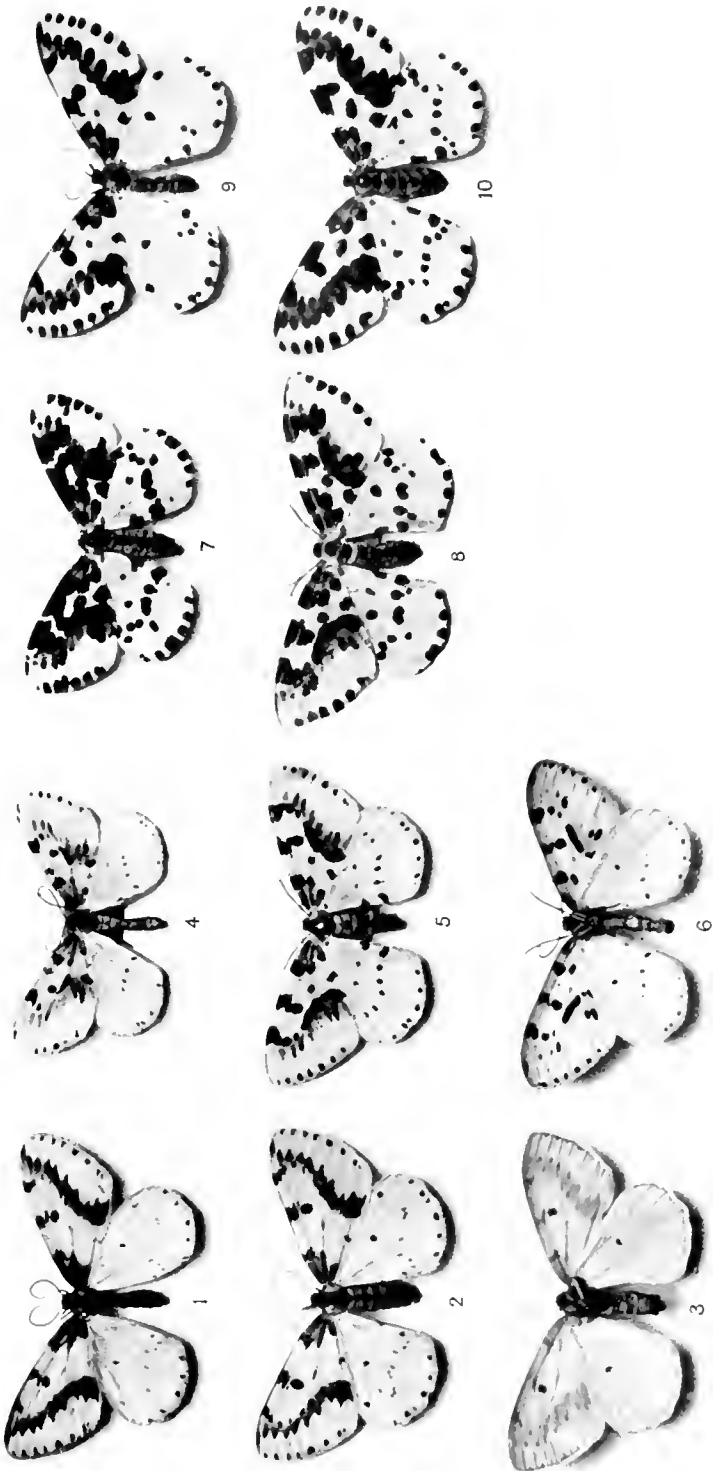
unisexual *lacticolor* stock; there is nothing in the hypothesis given above that would account for it.

One further speculation may be of interest—the form "*Q*" is in some respects so like *lacticolor* that one is inclined to wonder whether it may have been produced by the loss of a similar constituent from the normal *grossulariata*. But since the factor which turns *lacticolor* into *grossulariata* is sex-limited in transmission by the female while that which turns "*Q*" into *grossulariata* is not, on the hypothesis that Mendelian factors are borne by chromosomes, it must be supposed that the factor **G** is in the sex-chromosome while the factor **T** is in some other chromosome. It might be possible, therefore, for *lacticolor* to have arisen from *grossulariata* by the loss of some constituent of the sex-chromosome, while "*Q*" arose by the loss of a similar constituent from a different chromosome.

EXPLANATION OF PLATE XXX.

Figs. 1—3. *Lacticolor* ♂, ♀, and underside.

Figs. 4—6. "*Q*" ♂, ♀, and underside.

Figs. 7, 8. ♂ and ♀ of form with gap in the row of spots outside the yellow band; this form is possibly heterozygous for "*Q*."

Figs. 9, 10. Normal *grossulariata*, ♂ and ♀.

SOME NOTES ON THE LINACEAE.

THE CROSS POLLINATION OF FLAX.

By J. VARGAS EYRE and G. SMITH, B.Sc.

(From the Research Department, South-Eastern Agricultural College, Wye.)

WHILST testing a large number of species of Linaceae for cyanophoric glucosides during the past three years, it was observed that those species carrying white, blue or red flowers were more or less richly cyanophoric whereas the yellow flowered species, which for the most part exhibit an entirely different habit, failed to yield hydrogen cyanide and seemed to be devoid of cyanogenetic enzyme. During 1913 observations were made on a larger number of both blue and yellow flowered species and the previous observations have been confirmed. (Studies on Enzyme Action, xviii, *Royal Soc. Proc.*, B, vol. LXXXV, 1912.)

That the absence of cyanophoric glucoside and its enzyme is in any way correlated with the presence of the yellow pigment cannot be stated, but the fact that both glucoside and enzyme are absent from yellow flowered varieties led to the attempt being made to produce a yellow flowered flax containing glucoside or enzyme, or both[1], so as to throw light upon the question of the inheritance of Chemical Characteristics, and from this point of view the work has been extended. The present circumstances, however, are likely to cause a break in this work, and it is therefore considered desirable at this stage to place on record the observations which have been made.

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[1] The most complete information relating to hybrid flaxes appears to be contained in Graebner's *Synopsis der Mitteleuropäischen Flora* but, with the exception of the uncertain cross *L. salsoloides · alpinum*, the only cases referred to, namely *L. perenne · austriacum* and *L. narbonense · usitatissimum*, both due to Kolreuter (*Nov. Act. Acad. Sci. Petrop.* I. p. 339), do not afford the examples required.

The flowers of all the flaxes so far examined—numbering more than sixty—are hermaphrodite and although the flowers are slightly protandrous, when attempting to cross-fertilise it was found necessary to emasculate the buds.

The petals fall very readily when the buds are opened for the removal of the stamens. This of course deprives the stigmata of their protection, but seems to be in no way detrimental. It was found convenient therefore to discard the usual method of emasculation for the following. When the bud is advanced to within a day or so of opening, the tips of the petals were taken between the finger-tips and the corolla removed by a sudden jerk, thus exposing the stigmata and at the same time effecting the complete removal of the stamens. The stigmata, which at this stage are not receptive, apparently suffer no more by this somewhat rough treatment than by the more careful method usually employed; the bag by which they are covered affording sufficient shade and retaining the necessary moisture for their normal development, and we were able to convince ourselves by numerous trials that the stigmata were not pollinated by the removal of the stamens by this method[1].

Whilst testing the efficacy of this rough method of emasculation, a large number of flowers were so treated and kept covered without being pollinated. In every case the stigmata dried off and no sign of capsule development could be detected. This fact is recorded as showing that in the three species so treated, namely *L. perenne*, *L. flavum* and *L. maritimum*, seed is not normally produced parthenogenetically.

The flowers of some species of Linum, like those of the primrose, have styles of two different lengths, i.e., are dimorphic. This dimorphism is considered to be an adaptation favouring cross fertilisation and has been referred to by Darwin and others. Darwin[2] records that *L. perenne* yields no seed as a result of illegitimate pollination : we have not been able to confirm this but have found that when using this species of Linum about 30 per cent. of the short styled flowers produced seed capsules when " covered " owing to the pollen dropping on to the stigmata and very few of the long styled flowers set seed under the same conditions of isolation. It is probable that both types

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[1] After some practice it was found possible to use this method of emasculation successfully with long styled as well as short styled flaxes. Some care has to be exercised however in selecting buds in which the style has not become too elongated.

[2] *Forms of Flowers*, 1892, p. 89.

are capable of self-fertilisation because we have found that all flowers similarly treated and artificially pollinated by pollen from the flowers of the *same plant* set seed. This inference is supported further by the manner in which *L. perenne*, both short and long styled, set seed when "bagged" for the purpose of providing a supply of pollen for the trials we have made. In addition we have found that *L. perenne* ♀ carrying blue flowers with short styles when pollinated by *L. perenne* ♂ carrying white flowers with short styles produced seed normally and presented no difference from the case where a short styled blue flowering *L. perenne* ♀ was pollinated by a long styled *L. perenne* ♂ having white flowers.

The first attempt to effect a crossing between a Linum which contains glucoside and enzyme and one which does not—the main object of this work—was made in 1913 with *Linum monogynum* ♂ (Forster), a native of New Zealand, which is not dimorphic and *Linum flavum* (Linn.) ♀, a yellow flowered perennial plant which is dimorphic. Although tried repeatedly this cross seemed impossible to effect. The reciprocal cross, *L. flavum* ♂ and *L. monogynum* ♀ was however found to be successful, the ovaries of *L. monogynum* developed normally and each of the three capsules finally obtained contained three or four seeds; but this small number of seeds per capsule seems to indicate that fertilisation is difficult, and although the ten seeds obtained appeared to be quite normal not one of them germinated.

Linum maritimum, a dimorphic, tall yellow flowered species, was pollinated by *L. perenne*—both the blue and the white varieties—but without success; nor was the reciprocal cross any more successful. Concurrently with these attempts to hybridise the yellow flowered species, others which were in flower were also tried. It has been mentioned already that the white and blue varieties of *L. perenne* cross very readily, and this gave rise in the F_1 generation to plants bearing large pale blue flowers veined by darker blue. This fact is interesting as it may throw some light on the origin of some of the numerous varieties of *L. perenne* which now exist. *L. perenne*—both the blue and the white—was pollinated by *L. grandiflorum*, the common red species of the garden, but although every care was taken to use fresh pollen and to pollinate only receptive stigmata, no fertilisation was effected.

L. monogynum was pollinated by *L. grandiflorum* and all the ovaries commenced to swell, but before they were half developed a number of them had fallen and only a few matured: these on being opened proved to be seedless. To explain the cause of this growth it seems necessary

to assume that the pollen lived and gave some stimulus to the carpels but failed owing to some morphological or chemical obstacle to reach the ovules. Such stimulation of the ovaries without fertilisation is known to occur in other orders of plants.

In 1914 renewed attempts were made to fertilise the yellow flaxes by pollen from flaxes containing enzymes and glucosides. In the case of *L. arboreum* (Linn.), a species which resembles *L. flavum* (Linn.) but differs by its shrubby habit, more woody stem and its glaucous leaves, two hundred trials were made with pollen from *L. monogynum* (Forst.), upwards of one hundred trials with pollen from *L. narbonense* (Linn.), fifty trials with *L. austriacum* (a variety of *L. perenne*) and one hundred and fifty trials with blue flowering *L. perenne*, and in no case was any positive result obtained. Although the stigmata remained perfectly healthy no swelling of the ovaries took place. Attempts were made again to effect a cross between *L. flavum* (Linn.) and *L. monogynum* (Forst.), but in none of the one hundred and fifty trials made did fertilisation of the *L. flavum* take place and fifty attempts to effect the reciprocal cross, *L. monogynum* ♀ with *L. flavum* ♂, only gave one capsule containing one seed which did not germinate. Our efforts to fertilise *L. narbonense* by *L. monogynum* and by *L. arboreum* were no more successful and more than one hundred trials to pollinate blue *L. perenne* by *L. arboreum* and by *L. monogynum* were equally unsuccessful. Similarly when white flowering *L. perenne* and *L. austriacum* were employed for pollinating *L. arboreum* no fertilisation ensued. The pollination of *L. monogynum* by *L. arboreum* appeared at first to have been successful; most of the two hundred trials made resulted in early swelling of the ovaries and capsule development set in, but after about three weeks all but three capsules had dropped off and of those which remained one contained no seed, one contained ten seeds and the other three seeds. From these eleven plants have been raised, the foliage of which resembles that of *L. monogynum* both in general appearance and in containing both enzyme and glucoside associated with that species. So far these plants have shown no signs of flowering, and in this respect they differ from seedlings of *L. monogynum* raised at the same time.

Some two hundred trials were made to secure a cross between *L. monogynum* ♀ and *L. narbonense* ♂ and of these quite half exhibited swelling and the capsules remained on the plant for some time. Finally however only three capsules remained and these yielded two and three seeds in each. From these only three plants could be

raised which again only differ from *L. monogynum* in that they show no signs of coming into bloom.

In addition to these experiments with isolated plants observations have been made of the character of the plants raised out of doors on a number of plots where considerable quantities of different varieties of flax have been grown. These variety trials of commercially grown seed have been conducted during several years and have afforded an opportunity for watching any changes which might occur in the character of any particular variety.

It has been mentioned already in a previous publication (*loc. cit.*) that in certain flax-growing districts the opinion prevails that flax is unstable, readily losing certain of its characters when grown repeatedly in those regions. It is stated for example in certain parts of Central Russia that besides changes in habit, the colour of the flower changes. Little information of a reliable character bearing on these points being available and in view of their importance in connection with attempts which have been made concurrently with this work to isolate improved strains of flax for commercial purposes, it was decided to make use of the material at hand to test the truth of these statements.

On many of the flax plots grown in 1912 it was observed that a small proportion of white flowering plants accompanied those bearing blue flowers, whereas on other plots the plants were either entirely blue or entirely white flowering. When the seed from the white flowering plants accompanying the blue were collected separately, without "bagging," and sown in 1913, plants bearing white flowers only resulted, and seed collected from the blue flowering plants gave only blue flowers. Examples of this kind were met in the case of *L. usitatissimum* from Vologda, Pskoff and Holland, and also in the case of the so-called varieties of this species, namely *L. chamissonis* from Valencia, *L. multiflorum* from Heidelberg and several others.

Besides this difference in the colour of the flowers there was noticed also with some of the varieties grown a difference in the depth of the colour of the flowers, some being of a darker shade of blue than others which occur alongside on the same plot. *L. floccosum* furnished one example of this kind, and the large seeded variety of linseed which is imported from N. Africa another example, where a difference in the intensity of colour extends not only to the flowers but also to the foliage of the plant : some bearing pale green, others dark green leaves.

Seed of *L. pallescens* obtained from Madrid gave an uniform crop of pale blue flowering plants in 1912 when grown at The John Innes Institute at Wimbledon, but the seed saved from that crop and grown at the South-Eastern Agricultural College at Wye during 1913 gave rise to a mixed crop; some few plants bearing white flowers and the others pale blue flowers similar to those of the 1912 crop. The seed saved from the white flowering plants gave in the next year (1914) mostly white flowering plants, accompanied by a few bearing pale blue flowers. The seed saved from the pale blue flowering plants gave in 1914 only pale blue flowering plants. Other instances of change in the colour of flax flowers when grown in the open year after year under ordinary conditions have also been observed, an interesting one being afforded by *L. humile*, the seed of which was obtained from the Botanical Gardens at Madrid. This gave a mixed crop when grown in 1912 of dark blue, white and pale blue flowering plants. The seed saved from the dark blue flowering plants gave in 1913 plants bearing dark blue flowers only, and the seed saved from the white flowering plants gave only plants with white flowers in 1913. The seed saved from the pale blue flowering plants however gave a crop which consisted of pale blue, white and dark blue flowering plants in 1913. When the seed was saved and sown separately in the next year (1914) it was again found that seed from the dark blue flowering plants gave plants carrying dark blue flowers, and seed from the white flowering plants gave plants carrying only white flowers, whereas the seed saved from plants which had pale blue flowers again gave rise to plants having white, pale blue and dark blue flowers. In 1913 selected plants of *L. humile* were " covered," and the seed sown in 1914 when it was found also that the white came white, the dark blue came dark blue, and, as with the plants that were not " covered," the pale blue flowering plants gave rise to plants bearing dark blue, white and pale blue flowers.

These observations appear to afford an instance of the segregation of allelomorphic characters, expected when a hybrid is propagated from seed. This is of particular interest in view of the fact that both *L. usitatissimum* and *L. humile* very readily self-pollinate, and although not themselves dimorphic possess styles apparently as long as a long styled form in a dimorphic species.

The flaxes are sometimes regarded as "selfing" so readily that there is small chance of cross-pollination being effective. It seems quite clear however from the foregoing observations that this is not always the case and does not apply to the varieties of *L. usitatissimum* commonly

grown, and this view receives support also from the fact that dimorphism occurs among the species of Linum. It is noticed that the pollen is somewhat adhesive in character and is produced only in relatively small quantities, and it seems highly probable that the crossing which takes place is almost entirely caused by the insects which may be observed visiting the flowers freely.

The attempts being made to isolate improved strains of flax for commercial purposes have been referred to already. These are being conducted at Wye under the auspices of the British Flax and Hemp Growers' Society, and were commenced in 1912.

Flax is grown very extensively both for the seed it bears and for the fibre which is contained in the stem. The value of a flax crop when grown for the fibre depends mainly upon uniformity in height over the whole crop, tallness and branchlessness of the individual stems and upon the quantity of fibre they bear—the seed obtained from the crop being in this case of minor importance. In the case of a flax crop grown for seed its value depends mainly upon the quantity of seed produced and upon the oil-content of the seed obtained—the straw in this case being of relatively little value is frequently disregarded.

The sowing seed sold commercially for these purposes usually gives rise to crops which exhibit certain marked irregularities, and this is noticeable more particularly when flax is raised for fibre production. Generally speaking such crops are composed of tall and short growing plants, some of which carry much and some little seed, whilst many may be observed which exhibit a marked tendency to branch at the base instead of giving long single branchless stems.

The object has been to obtain from such mixed seed which usually comes on the market and from other sources some selected strains of seed more suitable for the economic production of fibre on the one hand and of seed rich in oil on the other.

With regard to raising improved strains for the latter purpose the work has not yet proceeded far enough to warrant anything definite being said, most attention, up to the present, having been devoted to exploring the possibilities of improving the flax fibre crop.

In the first year of this work (1912) the samples of seed which one of us had collected for the purpose in 1911 from particularly good flax fibre crops in various parts of Russia, Holland and Belgium, and also certain trade samples were grown at The John Innes Institution, where we were able to profit by the example of work of a similar nature which

13—2

was already proceeding at that Institution. From certain of these trial plots a number of plants were selected for tallness of branchless stem and absence of tillering, and these were "covered" separately. Some additional plants were selected from some of the same plots on account of their shortness of stem, and these were also "covered" separately. Under these circumstances of isolation seed set abundantly.

In the following year, 1913, the seed from the "covered" selected plants were sown at Wye, each seed being sown separately one foot apart in rows, which were also one foot apart so as to give each plant a full opportunity for displaying its true character. It should be mentioned also that throughout this work a method of labelling has been adopted which has maintained the identity of each of the plants originally selected.

When the plants raised in this manner were about to come into flower a similar selection was made again, and of the plants raised from selected tall parents only those plants were "covered" which had not tillered and which possessed relatively tall single stems—the measurements being made in every case from the ground level up to the lowest branch on the stem. In the case of the plants derived from selected short parents only short plants were selected and "covered." It appeared evident at this stage of the work that if tall plants and short plants are selected from one and the same crop, and these are properly "covered," and the seed resulting from the selfing of the covered plants is sown, tallness generally characterises the plants derived from tall parents and shortness those from short parents[1].

In 1914 a similar procedure was followed with regard to sowing the seed obtained from the "covered" plants of the previous year, and it was noticed again that plants selected for tallness and for shortness breed true to those characters—an average difference of about twelve inches in the height from the soil level to the first branch being observed between those plants resulting from a repeated selection for tallness and those repeatedly selected for shortness.

With the object of ascertaining how far these efforts to eliminate tillering had been successful and how far the general height of the crop was likely to be increased, reference plots were arranged alongside the plots of twice selected flax, upon which some of the various samples of seed originally employed in 1912 were grown under similar conditions regarding distance apart.

Upon making a comparison of the crop raised from the originally

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[1] *Vide Journ. Agric. Soc.* England, 1913, LXXIV, 140.

imported seed and the corresponding crop raised from the selected seed, it was at once apparent that an increase in the height had been brought about by selecting for tallness and the crops from the selected seed presented a greater degree of uniformity. The actual amount of the increase was found to vary with the different samples. In the case of one of the samples brought from Pskoff and another from the Province of Livonia an increase of nearly ten inches was manifest. In other cases the increase was not so marked, while with seed procured from the region of Minsk no increase in the height was noticeable.

With regard to tillering our efforts have not proved so successful. The accompanying figures represent some of the results obtained and are arrived at by taking some five hundred plants at random from the parent plots and a similar number from the selected plots, and counting those which had tillered and those which had not at the time of flowering.

Reference name of seed	Percentage of plants which tillered	
	Parent seed 1911 grown 1914	Selected seed grown 1914
Dutch II	87 per cent.	60 per cent.
,, III	93 ,,	70 ,,
Pskoff I	90 ,,	56 ,,
,, III	95 ,,	71 ,,
Livonian I	86 ,,	72 ,,
,, II ...	—	72 ,,
Vologda	89 ,,	78 ,,
Dedoviezy	89 ,,	70 ,,
Rsheff	96 ,,	66 ,,

Although the proportion of plants which tiller to those which do not has been reduced considerably, it appears that local conditions of soil play such an important part in conditioning this manner of growth that it would appear doubtful whether much more can be done in this direction.

Our thanks are due to Professor Bateson for guidance and assistance in several parts of this work.

NOTE ON EXPERIMENTS WITH FLAX AT THE JOHN INNES HORTICULTURAL INSTITUTION.

By W. BATESON, M.A., F.R.S.

In connexion with Dr Eyre's paper the following note of our experience with flax may be of interest. In 1911 Mrs Ryan of Fort William suggested to me that an improved strain of flax might be of value to the agriculture of Ireland and of the Scottish Highlands. As I had long intended to make experiments on heterostyly in flax I obtained some samples of seed. My interest in the subject was especially concerned with the possibility of crossing the homostyled *L. usitatissimum* with some heterostyled species such as *perenne*. Except in the style-structure and habit (*usitatissimum* being strictly annual) there is no noticeable distinction between the two species. Nevertheless all attempts to cross them, however made, have failed with us. In this respect there is nothing more to report. I may mention that I used the method of emasculation described by Dr Eyre, namely bodily removal of corolla with adherent anthers, very successfully in the case of the *short-styled perenne*, but did not find it applicable to any other forms.

Many samples of seed of *usitatissimum* were kindly sent by Messrs Vilmorin. I also received others (through Dr Hincheliff of the Department of Agriculture for Ireland) from Mr Ghekiere and from Mr de Zeeuw. Among the Irish samples was one that was said to have been saved for length of stem.

The plants in each sample were irregular in height, being obviously a mixture of several types. In most samples a few very tall plants occurred, reaching to about 4 feet, whereas the majority were about 3 feet high. I covered the flowers of one such tall plant in the sample sent by Vilmorin as "Courtrai," and fearing that there might be self-sterility I also put into one bag the heads of two such plants which

were growing close together. The event showed that flax is perfectly self-fertile. The seeds of the three tall plants gave in 1912 rows of plants most of which were of the 4 foot class. Many plants of course did not reach this height and there were several small plants, but I have little doubt that the smaller plants were merely prevented from reaching their full development by crowding. The subject seemed to be unsuitable for accurate investigation without very elaborate precautions to ensure uniformity of conditions and it was treated simply as a matter of economic interest. The height reached varies greatly with the nature of the soil and the spacing. In 1913 the seeds from the tall strain (bagged) gave plants averaging 4 ft. 6 in. with individuals 5 feet high, but this increase was obviously due to the ground chosen having suited them better; for the 1914 crop, similarly raised from them, was grown on inferior land and for the most part did not fully reach 4 feet. The 1915 crop, similarly raised from these, put on the land used in 1911 gave a very level crop 4 feet high.

The seed from the plants of 1914 which were *not* covered was collected in mass and sent to Mr F. K. Jackson, of the Leeds University Flax Experiment Station at Selby. In his Report for 1915 he says that after rain came at the end of June this flax "began to grow vigorously, and in a fortnight had outstripped all other varieties in the field, so that by harvest it was from 9 to 12 inches taller and much superior in quality." The weight of crop with the seed on was reckoned at 1 ton 13 cwt., that of the next best flax on the same land being 1 ton 8 cwt. 1 qr.

Evidently many points of genetic importance could be studied in this case by accurate methods. In 1915 Miss M. R. Michell began such work here, making crosses between plants of various heights, etc. Meanwhile it is to be noted that, as the result of our experience, the raising of a tall strain of flax is a very easy matter, and can be done by simple selection of materials already existing in common crops. I may add that at Selby in an ordinary crop growing on agricultural land I saw several individual plants clearly belonging to the tall strain, reaching about 4 feet.

To what extent crossing takes place under natural conditions I cannot say. Most seed presumably is the result of self-fertilisation. I saved seed from a white flowered variety not covered, growing between rows of blue flax, and all the plants except one came white. (There was *some* reason also for suspecting that even this one was a stray from the next row; for the plant agreed with that row, which

was of a peculiar type.) As white is recessive to blue in flax, these plants were probably from self-fertilised seed. In another case a curious dwarf form with dark blue flowers, about 1 ft. 10 in. high, was similarly tested. It had appeared originally as a single plant among crimson *L. grandiflorum*. Presumably this came from a stray seed. In general appearance this type somewhat resembled the oil flaxes of India. A quantity of seed of this variety, gathered from uncovered plants growing beside the other flaxes, came perfectly true to type. It is therefore to be presumed that the *usitatissimum* varieties are habitually self-fertilising, at least in England. On the other hand I cannot explain the fact that the seed sent from Ireland as saved for tallness did not give a crop in any way remarkable for height.

How many genetically distinct heights exist cannot be said. Besides the oil flaxes which are about 1 ft. 9 in. high we have had certainly three heights: (1) our own tall strain, about 4 feet; (2) several ordinary blue and also white forms, about 3 feet; (3) a dark blue, true-breeding type, about 2 ft. 6 in. Each of these is genetically pure, almost beyond question, and the rows of the several types standing side by side were each in general appearance strikingly level and uniform at their respective heights.

MENDELIAN INHERITANCE IN VARIETAL CROSSES OF *BRYONIA DIOICA.*

By W. NEILSON JONES, M.A. and M. CHEVELY RAYNER, D.Sc.

THE breeding experiments described in this paper were carried out as a result of observations made on plants of *Bryonia dioica* intended originally for experiments bearing on the inheritance of sex.

It is well known that species hybrids resulting from the crosses *B. dioica* × *B. alba* and *B. alba* × *B. dioica* are sterile (1, 2).

It has, moreover, been suggested that parthenogenesis occurs regularly in normal flowers of *B. dioica* (3, 4).

Our records agree with those of previous observers as to the sterility of these hybrids, but no experimental proof was obtained by us that parthenogenesis occurs in *B. dioica*, although a large number of flowers were covered and kept under observation.

It was thought possible that crosses of the species named with other members of Cucurbitaceae might yield further results, and with this end in view *B. dioica* and *B. alba* were used for reciprocal crosses with *Cucurbita Melo, Cucurbita Pepo* (3 vars.) and *Cucumis sativa.*

These crosses were all unsuccessful.

In one case, viz. *B. dioica* × *C. Melo*, fruit set and several seeds different in shape and colour from those of the seed parent were formed but did not germinate. In no case was viable seed obtained as a result of such species crosses.

In the course of these and of other experiments for which *B. dioica* was used, a side issue was raised which led to the breeding experiments described in the present paper.

The plants in our original cultures of *B. dioica* were obtained from three sources :

(*a*) Wild seedlings from the Lambourne Valley, Berkshire.

(b)   Seedlings raised from seed obtained from Erfurt, N. Germany.

(c)   Plants from tubers sent from an independent source near Erfurt (exact locality unknown).   The plants from sources (b) and (c) are identical and may be treated as belonging to one group.

These two lots of plants {(a) and (b) + (c)} differed from one another in respect to a number of characters relating to general habit, shape of leaf and structure of flower and fruit.

The differences being constant and equally well-marked in all plants of the same "variety," individual plants were "selfed" and "crossed" in order to determine the genetical behaviour of these distinguishing characters.

It was found that plants "bred true" to type, and that the characters investigated—while showing fluctuation about a mean—are not appreciably affected by cultural treatment.

There can be no doubt, therefore, that two distinct varieties or *petites espèces* of Bryony are concerned and that plants belonging to either group may be readily distinguished one from the other.

For the sake of brevity these two varieties will be known throughout this paper as *B* (native seedlings, (a) in category on p. 203) and *G* (German seedlings or tubers, (b) and (c) in category on p. 204).

The characters selected for investigation as being most susceptible of measurement were:

A.   Bloom on the berry.

B.   Number of stigma-branches and placentae in the ovary (*i.e.* number of carpels).

C.   Number of vascular bundles in the stems.

D.   Habit and leaf-shape.

It is fully realized that the number of plants available is not sufficient to give satisfactory ratio numbers, especially in cases such as number of carpels (see below).

It is nevertheless believed that the data are sufficient to establish the general mode of inheritance and to show clearly:

(a)   That within the limits of a so-called "species" a number of varieties occur differing from one another in characters that are inherited according to Mendelian rules.

(b)   That it is therefore possible to produce new combinations of such characters artificially.

(c)   That there is need for caution by systematists in distinguishing new species, especially in the case of large genera, e.g. *Rosa*, *Rubus*, etc., in which there is a tendency to multiply number of species to an inordinate extent.

It appears likely from an analysis of the results obtained from crossing two such forms in Bryony, that many of these so-called "species" are natural hybrids which occur as segregates from intercrossing among a comparatively small number of forms which breed true to type.

The genetical behaviour of the differentiating characters cited above will now be considered.

A.   *Bloom on the berry* (5).

The ripe berries of the two varieties B and G differ in that the berry of G is scarlet with a shining surface, while that of B is dull crimson in colour with a heavy waxy "bloom."

The difference in colour is due to a superficial deposit of wax which can be removed by washing in alcohol.

The essential external difference between the berries is, therefore, the *presence* of "bloom" in variety B and its absence in variety G.

Genetical behaviour.

The hypothesis which satisfies the facts most simply is that *absence of bloom* (or shininess S) is an almost complete dominant over *presence of bloom* (s); presence and *absence* of bloom depending on the behaviour of a single factor.

Thus in the cross:

$$ss \ (B \text{ plant}) \times SS \ (G \text{ plant}) - (\text{or the reciprocal cross})$$

F_1 would give theoretically sS, all without bloom.

In agreement with this expectation neither of the two female plants obtained from this cross had berries with "bloom."

In F_2 expectation gives the following:

(a) $SS (G) \times Ss (F_1)$

$1SS$: $1Ss$

all without bloom

Experimentally, the nine ♀ plants obtained from this cross were all without bloom.

(b) $Ss (F_1) \cdot Ss (F_1)$

$$1SS \quad : \quad 2Ss \quad : \quad 1ss$$

$$\underbrace{3 \text{ no bloom}} \quad : \quad 1 \text{ bloom}$$

In actual experiment, the nineteen ♀ plants obtained from this cross are recorded as follows:

TABLE I.

No bloom	Slight bloom	Bloom
14	2	3
14	:	5

Thus absence and presence of bloom on the berry behave as a pair of allelomorphs and segregation of a typical Mendelian kind occurs in the F_2 generation.

The fact that there is variation in the amount of bloom in F_2 plants suggests however that the matter may not be so simple as is represented above, and that more than one factor may be involved.

B.   *Number of carpels* (6).

The ♀ flowers of the two varieties differ in several details of structure, of which the most notable affects the number of placentae on the ovary wall, and the correlated number of stigma-branches.

The ♀ flowers of variety B have 3 stigma-branches and 3 placentae with 3 groups of ovules; those of variety G have 2 stigma-branches and a corresponding number of ovule groups.   (Figs. 1, 2, 3, 4.)   Minor differences affecting size and shape of the corolla have been ignored in this investigation: the number of carpels concerned in the formation of the pistil as indicated by the number of placentae and of stigma-branches is the feature to which attention has been specially devoted.

The internal morphology of the ovary of Bryony is peculiar, and need not be discussed here beyond a statement to make clear the nature of the differentiating features.

Owing to the distribution of the vascular tissue associated with the placentae, the ovaries in transverse section give an appearance of

septation into *two* and *three* chambers respectively, the cavity of the
chambers being filled with delicate parenchyma, in which the ovules—
arising parietally in two or three groups on the ovary walls—are
embedded.

For the sake of brevity these two types of ovary will be spoken
of hereafter as two-carpellary and three-carpellary respectively, the
assumption being made that the number of stigma-branches and of
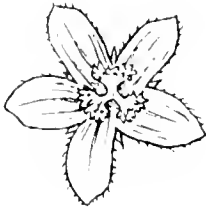
Fig. 1 *a*.   ♀ flower of *B. dioica*, var. *B*,
seen from above, showing three-
branched style.

Drawn with the aid of a camera lucida.
 × 2·65.
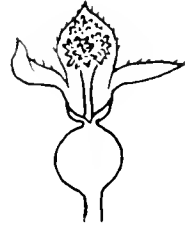
Fig. 1 *b*.   Sectional view of ♀ flower
of *B. dioica*, var. *B*, showing three-
branched style.

Drawn with the aid of a camera
lucida.   × 2·65.
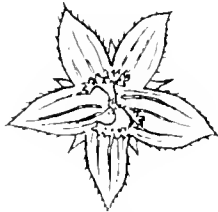
Fig. 2 *a*.   ♀ flower of *B. dioica*, var. *G*,
seen from above, showing two-
branched style.

Drawn with the aid of a camera lucida.
 × 2·65.
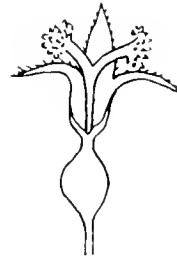
Fig. 2 *b*.   Sectional view of ♀ flower
of *B. dioica*, var. *G*, showing two-
branched style.

Drawn with the aid of a camera
lucida.   × 2·65.

ovule groups present in each case correspond to the number of carpels
concerned in the formation of the pistil.

As will be seen from the records below, the same plant may bear
both two-carpellary and three-carpellary flowers, but the proportional
numbers of the two kinds of flowers are constant, on the average, for

0·1 mm

Fig. 3. Transverse section across ovary of ♀ flower of *B. dioica*, var. *B*, showing the three-carpellary condition. Details as in Fig. 4.

Camera lucida drawing.

0·1 mm

Fig. 4. Transverse section across ovary of ♀ flower of *B. dioica*, var. *G*, showing the two-carpellary condition. *o* = ovule ; *vb* = vascular bundles.

Camera lucida drawing.

any one plant. Thus, in counts of two B plants the ratio of two-carpellary to three-carpellary ovaries was in one case 2 two-carpellary to 123 three-carpellary : in the other case 3 two-carpellary to 100 three-carpellary. In variety G 100 two-carpellary to 3 three-carpellary is the usual kind of ratio.

In F_2 plants from the cross $B \times G$ almost every possible variation in the ratio of twos to threes occurs.

This suggests that more than one factor is involved. In what follows two factors, G_1 and G_2, are assumed as a working hypothesis both of which tend to make the ovary two-chambered: thus, a G plant has, in respect to this character, the constitution $G_1G_1G_2G_2$ and a B plant has the constitution $g_1g_1g_2g_2$.

When G_1G_2 and g_1g_2 are present in equal amounts the ovary is equally likely to be two-carpellary or three-carpellary.

The number of fruits examined for each ♀ plant during 1913 and 1914 was about 450, though in many cases the number was considerably greater.

The percentage of twos present in the total number counted was adopted as a convenient method of expressing the results for comparative purposes.

In view of a possible criticism that the ratio of twos to threes may vary with cultural conditions or age and vigour of the plants, it is of interest to notice how closely the observations of the two years—made quite independently—agree with one another in most cases. This is illustrated in Table II, which gives the percentage of twos among the eighteen ♀ plants of the family obtained from the cross

$$F_1 \times F_1 \{(B \text{ plant} \times G \text{ plant}) \times (B \text{ plant} \times G \text{ plant})\}.$$

The other families yield like results.

It should perhaps be stated here that the figures of the last column, representing summation of the results for two successive years, are those used in the analyses below.

The genetical results may be summarised as follows :

Number of carpels: genetical behaviour.

F_1.   *Theoretical.*

$$g_1g_1g_2g_2 \ (B \text{ plant}) \times G_1G_1G_2G_2 \ (G \text{ plant})$$
$$|$$
$$F_1 \text{ all } G_1g_1G_2g_2.$$

From this it may be expected that in the absence of G_1 and G_2 factors in predominating amounts, there is about an equal likelihood that the ovaries in F_1 will be two-carpellary or three-carpellary.

TABLE II.

| | Percentage of *twos* in totals for | | |
Name of plant	1913	1914	1913+1914
15/11 *b*	28	28	28
15/11 *c*	55	40	50
15/11 *d*	57	62	60
15/11 *g*	79	70	74
15/11 *i*	30	30	30
15/11 *l*	43	29	38
15/11 *n*	72	76	74
15/11 *p*	81	92	87
15/11 *r*	67	65	66
15/11 *s*	40	40	40
15/11 *u*	58	49	56
15/11 *v*	2	0	1
15/11 *w*	56	plant dead	56
15/11 *x*	20	35	30
15/11 *y*	51	48	50
15/11 *z3*	9	8	8
15/11 *z4*	17	12	14
15/11 *z5*	26	34	28

Experimental.

In fact, the percentages of two-carpellary flowers on the two ♀ plants of this cross were 55 per cent. and 35 per cent.

From experimental results, therefore, the percentage of two-chambered ovaries to be expected in plants of the above constitution will be between 55 per cent. and 35 per cent.

F_2 (*a*).   *Theoretical.*

$$G_1G_1G_2G_2 \text{ (}G\text{ plant)} \times G_1g_1G_2g_2 \text{ (}F_1 \text{ plant)}$$

$$G_1G_1G_2G_2 \qquad G_1G_1G_2g_2 \qquad G_1g_1G_2G_2 \qquad G_1g_1G_2g_2$$

i.e., hypothetically there will be four types of plant in F_2 occurring in equal numbers.

Experimental.

In actual experiment the nine ♀ plants resulting from this cross bore the percentages of two-carpellary flowers shown in Table III, the hypothetical constitution of each group of plants being appended in each case.

TABLE III.

Showing result of cross G plant ($G_1G_1G_2G_2$) ⨯ F_1 plant ($G_1g_1G_2g_2$).

Name of plant	Number of plants in each class	Percentage of two-carpellary flowers	Theoretical constitution	Theoretical number of plants in each class
19/11 *f*	1	88	$G_1G_1G_2G_2$	2·25
19/11 *b* 17/11 *k* 19/11 *e*	3	82 80 76	$G_1G_1G_2g_2$	2·25
19/11 *g* 19/11 *a*	2	68 67	$G_1g_1G_2G_2$	2·25
17/11 *j* 17/11 *l* 17 11 *d*	3	55 39 37	$G_1g_1G_2g_2$	2·25

Of these four types, the only one which has appeared previously is $G_1g_1G_2g_2$, which is the constitution assigned to the two plants of F_1.

In the F_1 plants the percentages of two-carpellary flowers lay between 55 per cent. and 35 per cent.

The percentages of two-carpellary flowers on the three plants of F_2 of this constitution fall well within these limits. (Table III, plants 17/11 *j*, 17 11 *l*, and 17/11 *d*.)

F_2 (*b*). *Theoretical.* The heterozygote F_1 selfed should give plants having the constitution shown below in the proportions stated.

$$G_1g_1G_2g_2 \text{ (F_1 plant)} \times G_1g_1G_2g_2 \text{(F_1 plant)}$$

$$1G_1G_1G_2G_2 : 2G_1G_1G_2g_2 : 2G_1g_1G_2G_2 : \begin{cases} 1G_1G_1g_2g_2 : 2G_1g_1g_2g_2 : 2g_1g_1G_2g_2 : 1g_1g_1g_2g_2 \\ 4G_1g_1G_2g_2 \\ 1g_1g_1G_2G_2 \end{cases}$$

(See also Table IV, below, 4th column.)

Experimental.

The percentages of two-carpellary flowers borne by the twenty plants of the F_2 generation from the cross $F_1 \times F_1$ are shown in Table IV,

the hypothetical constitution of each group of plants being appended in each case.

TABLE IV.

Showing result of cross F_1 *plant* $(G_1 g_1 G_2 g_2)$ F_1 *plant* $(G_1 g_1 G_2 g_2)$.

Name of plant	Number of plants in each class	Percentage of two-carpellary ovaries	Theoretical constitution	Theoretical number of plants in each class
15/11 p	1	87	$G_1 G_1 G_2 G_2$	1·25
{ 15/11 u } { 15/11 g }	2	{ 74 } { 74 }	$G_1 G_1 G_2 g_2$	2·5
15/11 r	1	66	$G_1 g_1 G_2 G_2$	2·5
15/11 d 15/11 u 15/11 w 15/11 c 15/11 y 16/11 d 15/11 s 15/11 l	8	60 56 56 50 50 47 40 38	$G_1 G_1 g_2 g_2$ $4 G_1 g_1 G_2 g_2$ $g_1 g_1 G_2 G_2$	7·5
15/11 i 15/11 x 15/11 $z5$ 15/11 b	4	30 30 28 28	$G_1 g_1 g_2 g_2$	2·5
16/11 y 15/11 $z4$ 15/11 $z3$	3	18 14 8	$g_1 g_1 G_2 g_2$	2·5
15/11 v	1	1	$g_1 g_1 g_2 g_2$	1·25

Our assumption as to constitution obtains confirmation in that the percentages of two-carpellary flowers in types $G_1 G_1 G_2 G_2$, $G_1 G_1 G_2 g_2$, $G_1 g_1 G_2 G_2$, $G_1 g_1 G_2 g_2$ of this cross agree reasonably well with the percentage figures for plants of the same constitution from the other cross (Table III, p. 211). This is shown graphically in Table V.

Accepting our hypothesis, therefore, it may be assumed that plants of the constitution $G_1 G_1 G_2 G_2$ bear flowers of which, on the average, 84 per cent.–100 per cent. are two-carpellary; plants of the constitution $G_1 G_1 G_2 g_2$ bear flowers of which, on the average, 71 per cent.–83 per cent. are two-carpellary, and similarly for the other types as shown in Tables III, IV and V, with doubtless a certain amount of overlapping between the different classes.

TABLE V.

Chart showing percentage of two-carpellary fruits in two varieties of Bryonia dioica and the F₁ and F₂ generations obtained by crossing them.

Explanation of Chart.

The diagram shows:

(1) Percentage of two-carpellary ovaries in *B* and *G* varieties.

(2) Hypothetical constitution of the various types, together with the presumed range of variation in percentage of two carpels in each type.

The diagram shows that the plants from all the crosses fall remarkably well within the limits of the various hypothetical types and that the expected types are all represented.
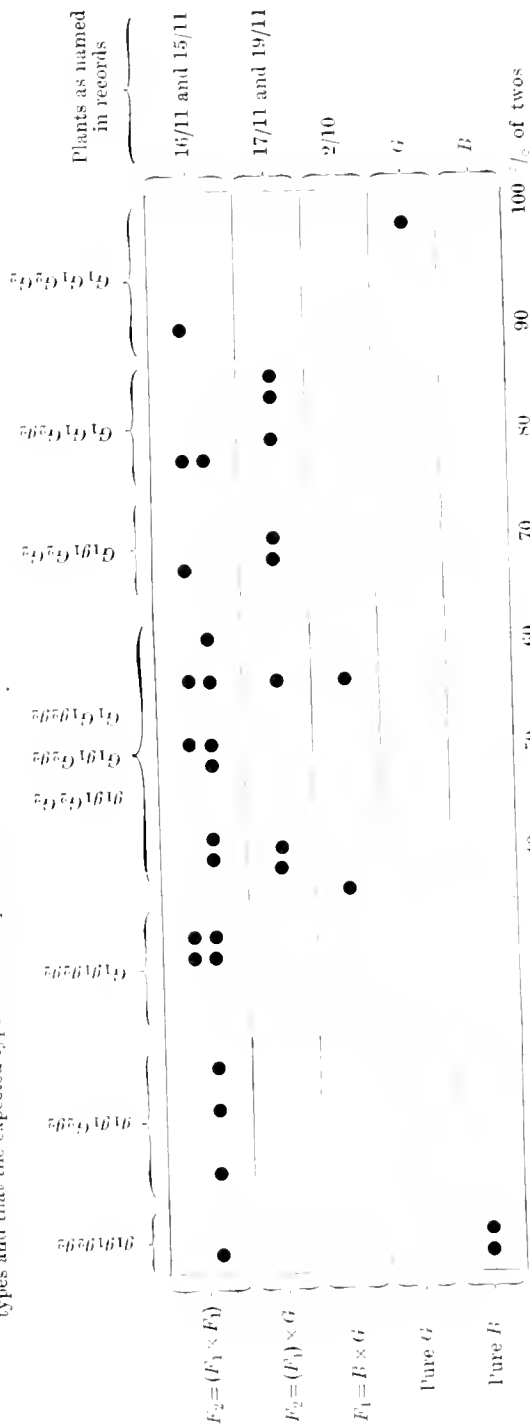
These results are exhibited in Table VI.

TABLE VI.

Hypothetical constitution	Average percentage of two-carpellary ovaries per plant
$G_1 G_1 G_2 G_2$	100–84
$G_1 G_1 G_2 g_2$	83–71
$G_1 g_1 G_2 G_2$	70–63
$\left\{ \begin{array}{c} G_1 G_1 g_2 g_2 \\ G_1 g_1 G_2 g_2 \\ g_1 g_1 G_2 G_2 \end{array} \right.$	$\left\{ \begin{array}{c} \\ 62–33 \\ \end{array} \right.$
$G_1 g_1 g_2 g_2$	32–23
$g_1 g_1 G_2 g_2$	22– 6
$g_1 g_1 g_2 g_2$	5– 0

The following comments may be made on the recorded figures and on the interpretation suggested for them:

(1) Since any one plant in successive seasons shows practically the same ratio of two-carpellary to three-carpellary ovaries, this ratio must presumably be of a definite fixed value and must be determined by a certain definite combination of factors, i.e. it is not due to any appreciable extent to the action of environmental conditions.

(2) The wide range in value shown in this ratio among the plants of a family such as $F_1 \times F_1$ (Table IV, p. 212) indicates that more than *one* factor is probably concerned. On quite other grounds this seems likely to be the case.

It is probable, for instance, that tendencies towards reduction in number of ovules and reduction in number of carpels may be simultaneously manifest in certain groups of plants, especially in Sympetalae (7).

In the case under discussion it may be that a factor concerned with the number of placentae in the ovary interacts with another which determines the number of ovules produced, the two sets of factors being jointly responsible for the condition found in the mature ovary.

The action of two factors has been hypothesised in order to show the *kind* of explanation which may be attempted, without prejudice to the employment of more than two factors.

Many more plants than those available would be required in order to determine this point.

C. Anatomy of Shoot.

In transverse sections of the aerial shoots of *B. dioica* the vascular bundles—which vary considerably in size in different regions of the stem—are arranged in two rings.

This arrangement is a general one in the Natural Order Cucurbitaceae and the anatomical details have been described for various genera including *Bryonia* (8, 9).

The total number of bundles is recorded as 10 for various genera, but deviations from the 5 + 5 arrangement are noted, and de Bary (10) mentions seven as the characteristic number in the outer ring of bundles in *B. dioica.*

The stems are ridged externally to correspond with the number of bundles in the outer ring, and the number of bundles in cross section can be readily determined by examination with a pocket lens.

We have found a constant and distinctive difference with regard to the number of stem bundles in our varieties, and have recorded their genetical behaviour when bred together.

At the base of the shoot close to the tuber, the total number of bundles is small—often eight or fewer.

As the distance from the tuber becomes greater, the number of bundles present in transverse section increases gradually to a maximum, the arrangement in two rings being maintained.

These maxima differ in the two varieties under consideration, this statement being based on a large number of observations on many different plants.

In variety *G* the number of bundles gradually increases up to ten, arranged in two rings of five each. However long or vigorous the shoot, this number is not exceeded in any part of the successive internodes. Fig. 5 (*c*).

In variety *B*, on the other hand, the number of bundles increases to 14 arranged in two rings of seven each.   Fig. 5 (*a, b*).

Correlated with this difference in number, the external ridges on the stem are respectively five and seven for the two varieties.

The possession of a shoot or some part of a shoot having fewer than 14 bundles does not preclude a plant from belonging to variety *B* in this respect.   Fig. 5 (*b*).

The difference between the two varieties lies in the capacity of variety *B* to increase the number of bundles beyond ten as seen in transverse section.   Although every shoot on the plant may not show

the 7 + 7 arrangement, a majority always do so, and practically all shoots on the plant will be found to possess more than ten bundles.

Records and careful drawings of serial sections through successive nodes and internodes have not provided any simple clue as to the significance of the 7 + 7 arrangement as compared with the other, and the condition is evidently a complicated one anatomically.
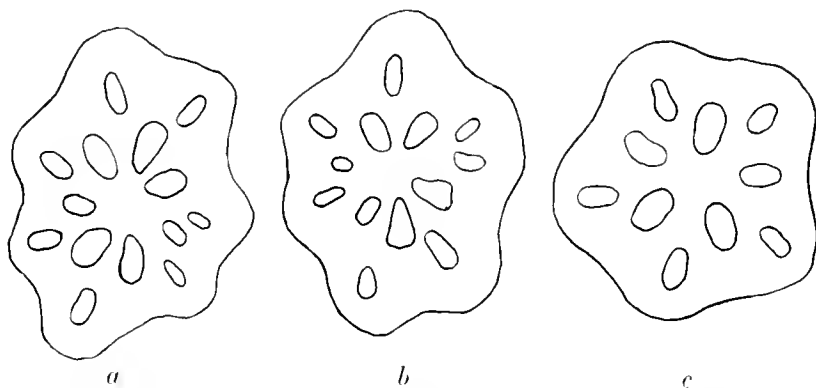
Fig. 5. *B. dioica*, vars. *B* and *G*. Transverse sections of stem internodes; *a* and *b* from variety *B*; *c* from variety *G*.

Camera lucida drawings.

The branching and anastomoses of the vascular strands become very complex at the nodes, and a detailed investigation of this region has not proved of any service in the investigation. A very short distance above or below the node, the arrangement of bundles typical for the variety is re-established.

Genetical behaviour.

If *F* be a factor conferring a capacity to increase the number of bundles beyond ten, then the facts would be satisfied if *F* were dominant over *f* (a capacity for increasing the number of bundles up to but not beyond ten).

Theoretical.

$$FF \text{ (}B \text{ plant)} \times ff \text{ (}G \text{ plant)}$$
$$F_1 \text{ all } Ff$$

Experimental. Of four plants from this cross, three had 14 bundles, one had 11–13 bundles.

F_2 (a).   *Theoretical.*

$$ff \text{ (G plant)} \times Ef \text{ (F_1 plant)}$$

$$1\,Ef \quad : \quad 1\,ff$$
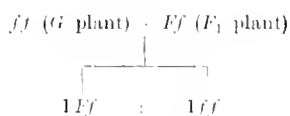
Experimental.   The results of this cross are shown in Table VII.

TABLE VII.

	10 bundles	11—13 bundles	14 bundles
No. of plants	10	8	1
	10	:	9

F_1 (b).   *Theoretical.*

$$Ef \text{ (F_1 plant)} \times Ef \text{ (F_1 plant)}$$

$$1\,FF \quad : \quad 2\,Ef \quad : \quad 1\,ff$$

$$3$$
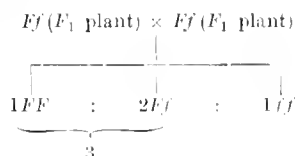
Experimental.   This cross gave plants with anatomy as shown in Table VIII.

TABLE VIII.

	10 bundles	11—13 bundles	14 bundles
No. of plants	9	27	2
	9	:	29

The two ♀ plants which were used as seed parents for F_1 both had the typical 7 + 7 arrangement of bundles.

D.   Habit and foliage.

The foliage of White Bryony is notoriously polymorphic, and much variation occurs on any one plant with regard to shape and incision of the leaves.

In spite of this considerable individual variation the two "varieties" under discussion have habit and foliage so unlike that they may be recognised at a glance.   (Plate XXXI, figs. 1, 2.)

In the F_2 generation obtained subsequent to crossing so many combinations occur that, with the number of plants at our disposal, it is impossible to say more than that segregation undoubtedly takes place.

Extracted types, with leaves identical in shape, colour and incision with those of the original parents, are shown in the photographs in Plate XXXIII, figs. 9–12.

Of the parents, variety B has stems with comparatively shorter internodes, leaves dark-green in colour, rough and deeply-lobed. (Plate XXXI, fig. 3.)

Variety G has stem with—on the average—longer internodes, leaves paler in colour, smoother and less deeply-lobed. (Plate XXXI, fig. 3.)

The range of variation in leaf-shape among individuals of the two varieties is evident from the photographs, which make clear that although considerable variation in leaf-shape exists, and the most deeply-lobed leaf-type of variety G approximates to the least deeply-lobed type of variety B, no real overlapping of the two types occurs. (Plate XXXII, figs. 4, 5.)

If the *average* form of leaf is considered (which determines the appearance of the plant as a whole), the two varieties are widely different.

In the F_1 generation of the reciprocal crosses $B \times G$ and $G \times B$ the foliage is intermediate in character with a bias towards the B type. The range of variation in leaves of F_1 is shown in Plate XXXII, fig. 6.

In the cross $F_1 \times G$ new types of foliage appear, and it is not easy to classify these new combinations, especially as the characters are not such as can be expressed numerically.

It may be said with certainty, however, that the pure G type of foliage can be extracted from this cross and that the pure B type does not appear. Shoots from a plant having this constitution are shown in Plate XXXII, fig. 8 c (17,11 l) with characters similar to those of the heterozygote.

When the heterozygote is selfed numerous types of foliage also appear, and among them individuals with the pure G and pure B type of leaf may be identified. (Plate XXXII, fig. 8, d and e, and Plate XXXIII, figs. 9–12.) The exact proportion of these "pure extracted" types is difficult to determine.

Although, as stated above, plants of the two varieties B and G show considerable range of variation in leaf-shape, the two classes do not overlap.

When, however, the pure forms are mixed with the numerous hybrids an almost continuous series of foliage forms is presented.

Thus, while it is possible to recognize a given plant as a typical representative of the G type of foliage, it may be almost impossible to

decide with certainty from appearances only whether another plant is one of the more extreme forms of G or a G-like type of hybrid. Only breeding tests could decide this satisfactorily.

It would seem therefore that, on crossing plants with the B and G types of foliage respectively, segregation occurs in the second generation resulting in the re-appearance of the original types and also of many intermediate hybrid forms—the range of variation in any type being such that overlapping occurs with those adjacent to it.

Independent observations during successive years indicate that the leaf-type of individual plants remains sensibly constant within a small range of variation, and that if it were possible to express the results more precisely, the different hybrid-types might be definitely recognized and distinguished.

Similar observations apply to the other vegetative characters mentioned, such as colour and texture of leaves, and degree of hairiness: plants showing the characters of the grandparents appear in the F_2 generation, together with a number of intermediate forms difficult to classify precisely.

Since several pure G and pure B plants occur in the family of 38 from the cross $F_1 \times F_1$, the factors determining leaf-shape are probably few in number, but no attempt has at present been made to analyse the ultimate anatomical characters which determine the shape, colour and texture of the leaves.

Records were made of the length of internodes on shoots of plants of both varieties and of their hybrids, but, up to the present, a simple method of presenting such records has not been devised.

It seems not improbable that the differences in length of internode, shape and texture of leaves, and number of vascular bundles in the stem internode may be closely correlated and connote a difference of phyllotaxy in the shoots of the two varieties. This point is not readily determined by external observations in a climbing plant and awaits an independent investigation.

Although the numbers of plants employed in these experiments were not sufficient to yield trustworthy ratio-numbers, the facts are believed to be of interest inasmuch as they point clearly to Mendelian inheritance of characters distinguishing plant forms of "sub-specific" rank; and following from this, they emphasize the pressing need for revision of systematic nomenclature when new species are separated on morphological characters alone, without reference to genetical behaviour.

The geographical distribution of these two varieties of Bryony may be of interest in connection with the history of the species as a member of the British Flora.

All the British specimens examined by us resemble type *B* as described in this paper, and this form has also been noticed by us in South Tyrol.

The plants of variety *G* were obtained partly from seed purchased from an Erfurt firm and partly from tubers sent from N. Germany (exact locality unknown), and the plants from these two sources are identical in every respect.

The fact that the two strains breed true to type and give so many hybrid types on crossing suggests that their geographical distribution may be discontinuous, but this point has been imperfectly studied and awaits further investigation.

This part of the enquiry has of necessity been abandoned temporarily owing to the war, and it is hoped that the publication of the paper in its present form may lead to the collection of further data bearing on geographical distribution from readers who may be interested in the facts described.

In a paper published in 1905 entitled "Parthenogenesis und Variabilität der *Bryonia dioica*" Bitter discusses the variability in size and shape of leaves, as also in size, colour and structure of flowers (corolla of ♀ flower), observable in plants of *Bryonia dioica* from various localities in Münster, under observation in connection with an investigation into the occurrence of parthenogenesis in the species.

He also remarks on the absence from the Floras of varietal forms distinguished on such characters.

Bitter describes and figures leaves and flowers from his cultures, the former being of interest in connection with the facts described in this paper, since they demonstrate the existence of our *B* and *G* varieties in Münster and also that of at least one of the more distinct hybrid leaf-types bred by us.

This author's observations on variability in size, shape and colour of flowers coincide with our own in many respects, and it seems likely that the plants he describes would have fitted easily into our scheme of inheritance.

Bitter's observations were mainly concerned with parthenogenesis, and he concludes tentatively that variability in *B. dioica* is directly

connected with the existence of facultative parthenogenesis and is comparable to that observed in *Alchemilla, Hieracium,* etc.

This possibility is of course not excluded by our results, but it seems unlikely that it is the most important cause at work.

Nothing is known at present of the cytology of parthenogenesis in Bryony—if it occurs—and seeds produced parthenogenetically are—according to Bitter and Focke—borne but rarely and in small numbers.

It seems, therefore, more reasonable to regard the varietal forms described as *biotypes* which, on crossing, give rise to fresh types by 'shuffling' and recombination of characters according to Mendelian laws (11).

SUMMARY.

The paper is concerned with the genetical behaviour of certain differentiating features in two distinct strains or varieties of *Bryonia dioica.*

The results obtained from breeding experiments may be summarized as follows :

1. *Bloom on the berry.*

Absence of a waxy bloom from the ripe berries of one variety behaves as a simple dominant to *presence of waxy bloom* on the berries of the other variety.

Presence and absence of bloom behave as a pair of simple allelomorphic factors.

2. *Number of carpels in ♀ flower.*

The proportion of two-carpellary to three-carpellary flowers, as evidenced by the number of stigma-lobes and of placentae in the ovary of the flower, in families of plants produced by crossing the two varieties, can be interpreted by assuming the co-operation of two factors.

3. *Anatomy of stem.*

The number of vascular bundles in transverse sections of the stem of one variety is typically 10 (5 + 5), and in the other typically 14 (7 + 7).

The capacity to increase the number of bundles beyond ten behaves as a simple dominant to absence of such capacity.

4.   *Habit and foliage.*

Differences relating to these features are evidently complex in origin and have not been adequately studied for complete analysis.

The following points have been determined:

(*a*)   Crossing leads to the production of a number of new types in the second generation.

(*b*)   Segregation occurs involving the reappearance of the original characters of the grandparents in the F_2 generation.

(*c*)   The number of factors concerned in the determination of leaf-shape is small—possibly two.

5.   The experiments on Bryony emphasize once more the need for caution in the sub-division of existing species without recourse to breeding tests.

A number of segregates showing morphological differences due to new combinations can evidently arise from the intercrossing of a few stable types within the limits of a so-called species.

The stability of these new forms can only be tested by breeding, and the extreme types among them may be connected by an almost continuous series of transition forms.

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        University of London.

University College,
        Reading.

G   B

Fig. 1.

B   G

Fig. 2.

B   G   F₁

Fig. 3.

PLATE XXXII

Fig. 5.

Fig. 1.

Fig. 8.
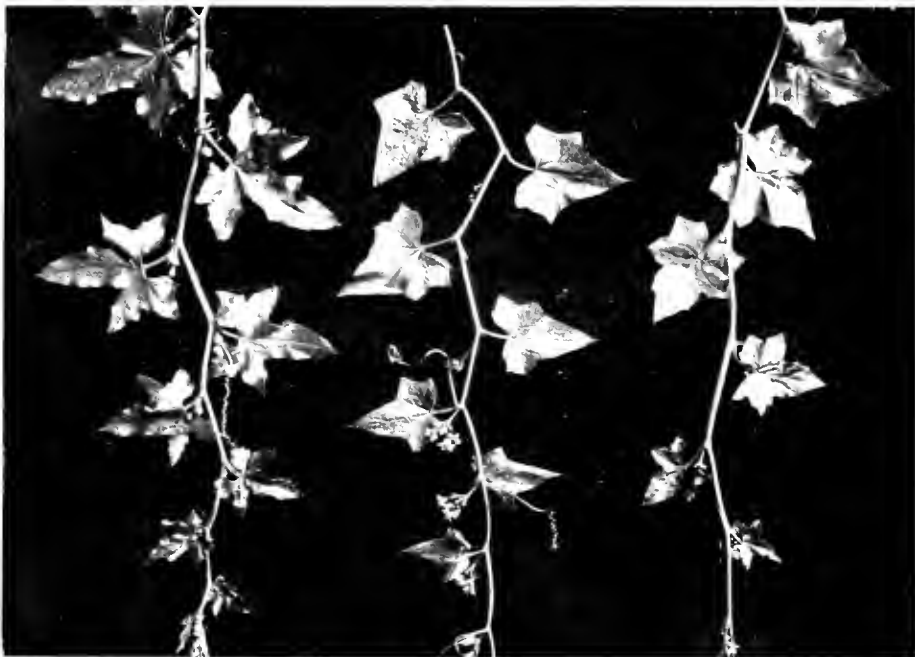
Fig. 7.

Fig. 6.

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Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12

EXPLANATION OF PLATES.

PLATE XXXI.

Fig. 1.   Plants of B and G varieties of *Bryonia dioica* growing side by side.

Fig. 2.   Ditto, nearer view.

Fig. 3.   Shoots of varieties B and G (original parents) and of hybrid F_1.

PLATE XXXII.

Fig. 4.   Leaves from plants of B variety showing extreme range of variation.

Fig. 5.   Leaves from plants of G variety showing extreme range of variation.

Fig. 6.   Leaves from plants of F_1 showing extreme range of variation.

Fig. 7 a.   Plant 15/11 $\cdot$3: a plant from the cross $F_1 \times F_1$ resembling heterozygote F_1 in leaf-character.

Fig. 7 b.   Plant 2/10 b: a plant from the cross $B \cdot G$ ($= F_1$).

Fig. 8 c.   Plant 17/11 l: a plant from the cross $F_1 \cdot G$.

Fig. 8 d.   Plant 15/11 h: a plant from the cross $F_1 \cdot F_1$ resembling G parent in leaf-character.

Fig. 8 e.   Plant 15/11 p: a plant from the cross $F_1 \cdot F_1$ resembling B parent in leaf-character.

PLATE XXXIII.

Fig. 9.   Plant 15/11 $\cdot$4: a plant from the cross $F_1 \cdot F_1$: resembles B parent in leaf-shape, bloom on berry and short-stalked inflorescence $=$ pure extracted B type for these characters.

Fig. 10.   Plant 15/11 r: a plant from cross $F_1 \cdot F_1$; resembles B parent in leaf-shape, but berry has no bloom and inflorescence is of G type.

Fig. 11.   Plant 15/11 b.   A plant from the cross $F_1 \times F_1$: resembles G parent in leaf-shape and absence of bloom, but inflorescence follows B parent.

Fig. 12.   Plant 15/11 w.   A plant from the cross $F_1 \times F_1$: resembles G parent in leaf-shape and absence of bloom and long-stalked inflorescence $=$ pure extracted G type for these characters.

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CONTENTS

THE SUPPRESSION OF CHARACTERS ON CROSSING.

By R. H. BIFFEN, F.R.S.,

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THE publication in a previous issue of this *Journal* of the paper "On the genetics of 'rogues' among culinary peas[1]," in which attention is called for the first time to a case in which a group of characters introduced by one of the original parents fails to affect the F_2 generation has led me to place a somewhat similar case on record in spite of the fact that the investigations dealing with it are still far from complete.

The character in this instance is the mouse-grey colour occurring in the glumes of the well-known Rivet wheat (*Triticum turgidum*). In this variety, and indeed in all of the grey-chaffed wheats I have been able to obtain up to the present, greyness is invariably associated with the presence of a quantity of silky hairs on the glumes so that all grey wheats are "rough-chaffed." The converse that all rough-chaffed wheats are grey however is not true, for white and red rough-chaffed varieties are moderately common.

Crosses between red or white rough-chaffed wheats and varieties with glabrous chaff show simple dominance of roughness followed by segregation into rough and smooth in the proportions of three of the former to one of the latter.

Where however roughness is associated with greyness, as for instance where Rivet wheat is used as a parent, the two characters tend to be coupled. In certain crosses with varieties of *Triticum vulgare* the coupling appears to be complete since all of the rough-chaffed forms occurring in the F_2 generation have grey chaff. In such cases the ratio for rough grey to smooth white is as $3 : 1$. However none of the F_2 generations have so far exceeded some 300 individuals so that there is the possibility that the expected smooth grey and rough white might occur if still larger numbers were raised. In another cross of the same

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[1] W. Bateson and Caroline Pellew, *Journ. of Genetics*, Vol. v. p. 13.

nature between Rivet wheat and Red Fife a different state of affairs is met with. The F_2 generation in this case contained black, grey and white-chaffed wheats. Several F_2's of this parentage have been raised, giving in all some 2000 plants, but the number is inadequate for a complete statistical examination, in view of the fact that a large percentage of the plants are sterile and consequently one cannot obtain much information from the F_3 generations. The most that can be said at present is that there are two classes of blacks, one rough and one smooth, corresponding forms amongst the white-chaffed individuals and no smooth greys.

Crossing the smooth black with rough white, the nearest approach so far possible to introducing one of the dominant characters on either side of the parentage, results in an F_2 generation showing coupling on a $3 : 1 : 1 : 3$ basis[1].

Crossing Rivet wheat with Polish wheat (*Triticum polonicum*) gives a totally different result to any of the crosses with *T. vulgare*. This wheat has white glumes which are so slightly hairy that they are generally described as glabrous. The glumes are further characterised by their enormous length which under ordinary conditions is some three times as great as that of any other wheat. The F_1 plants of this parentage, no matter which way the cross is made, have a pale grey chaff. Isabelline white is probably the most accurate description that can be given of the colour. It is not unlike that of the Polish wheat, but a faint grey tinge is present much as there is a tinge of blue in many white-flowered varieties of Campanulas derived from blue species. Thus the full dominance of grey seen in all of the other Rivet crosses is wanting.

The F_2 generations from these crosses differ altogether in their general character from the crosses with the varieties of *T. vulgare*. The latter are characterised by the occurrence of a bewildering, though evidently definite, series of unexpected forms such for instance as plants with bright grass green instead of glaucous foliage, with ears of the spelta type, with branching ears, dwarfs, etc. The former show no such features but merely individuals with the short or long glumes of the parents and a series of plants with an intermediate glume length. The short and the intermediate glumes are all markedly rough whilst the long-glumed forms are practically glabrous. Throughout the whole series containing over 2000 plants raised from 20 separate F_1's the glume colour was identical with that of the Polish wheat. In the

[1] Engledow, *Proc. Camb. Phil. Soc.*

following season 500 cultures, containing from 50 to 100 plants each, were raised from individuals of the F_2 generation and since then a few of the homozygous forms have been carried on to the F_6 stage. No counts of these later generations have been made but it is safe to say that the whole series of plants contained at least 100,000 individuals. Without exception the chaff colour was that of the Polish wheat. The number of plants dealt with appears to be sufficiently large to warrant the statement that in this case the grey chaff character has been totally suppressed.

One or two other coloured forms have recently been crossed with Polish wheat in the hope of finding similar cases but without success. Various red-chaffed wheats have given red F_1 plants and a normal segregation of three red to one white in the following generation whilst a smooth black wheat (from Rivet × Red Fife) has given a blackish F_1 segregating into blacks and white in the F_2. It promises to be of some interest however, for the colouring is confined to the plants with short or intermediate glumes. Further crosses made with homozygous forms of what may fairly be described as "alba" forms of Rivet wheat, from the cross Rivet × Polish, have merely behaved as ordinary white rough-chaffed wheats when crossed with smooth white varieties.

The suppression of the grey character occurring in Rivet wheat bears an obvious resemblance to the suppression of the type characters when the rogues of culinary peas are crossed with the type plants. There are however differences which may have some significance. The F_1 of rogue crossed by type or type by rogue shows clear signs of the type in the early stages of growth, though these gradually disappear and the plant becomes rogue-like and in future generations throws rogues only. In the case of the wheat no signs of the grey character can be detected at early stages of growth since this feature only develops at the stage in which the grains of the plants are practically mature. Further the colouring appears to be independent of any other features which can be recognised in the early stages of growth. In the peas there is other evidence pointing to the fact that the type characters are left behind in the base of the plant and consequently cut out of the germ lineage[1]. But in wheat there is no great difference either in the position or the date at which branches are formed. All of the branches are basal, arising at ground level from nodes so closely clustered together that they are almost unrecognisable. At first sight then similar phenomena can hardly be looked for. Yet it is possible they exist for

[1] Bateson and Pellew, *Proc. Roy. Soc.* Ser. B, Vol. LXXXIX. p. 174.

a solitary case has been met with where a rough grey wheat crossed with a smooth white has given F_1 plants bearing rough dark grey and rough white ears. The plants were well developed and thoroughly matured so that there can be no question of the genuineness of the phenomenon. The F_2 generation of this cross still has to be raised, and until this has been examined there must be some doubt as to whether similar phenomena are being dealt with.

In wheats it is possible that the suppression of characters is more general than it appears to be at present. A considerable number of examples are known where recessives make their appearance in F_2 generations from crosses of parents showing dominant characters only. Thus red-grained varieties crossed together frequently produce white-grained forms even though the parents breed perfectly true to their red colour. In the commonest cases the ratio of red to white is as 15 : 1. The ratio has been thoroughly established by Howard[1]. Nilsson-Ehle[2], who first called attention to the fact, has suggested that it is due to there being various red-producing factors C, C_1, C_2, etc. The parent wheats then have a constitution represented by Cc_1 and C_1c and the gametes of the hybrid form four classes CC_1, Cc_1, C_1c, cc_1. The combination of cc_1 with cc_1 will thus occur on the average once in sixteen times. Similarly by assuming the existence of three distinct red-producing factors, a ratio of one white to 63 red can be accounted for. Such proportions probably occur from time to time, but a wholly satisfactory demonstration of their existence has not been given up to the present.

On this hypothesis the highest frequency with which white can occur in such crosses is one in 16. But the ratio of one in four has recently been found in such a cross between Squarehead's Master and a deep red wheat collected in the western provinces of China and at present unidentified. The same cross and another between Squarehead's Master and a corresponding white form of this Chinese wheat has given bearded plants in the F_2 generation though both parents are beardless. The proportions are again approximately one bearded plant to three beardless.

It is possible that these cases represent terms in a series beginning with complete suppression of a dominant character, then its suppression once in 4 times, once in 16, once in 64, and so on, but it is difficult to devise methods for testing the hypothesis.

[1] Howard, *Mem. Dept. Agr. in India* (Botanical Series), Vol. v. p. 1, 1912.

[2] Nilsson-Ehle, *Kreuzungsuntersuchungen an Hafer und Weizen*, 1909, p. 68.

INHERITANCE OF ARTISTIC AND MUSICAL ABILITY.

By H. DRINKWATER, M.D., F.R.S.E., F.L.S.

THE investigation of the mode of inheritance of human traits has been confined, for the most part, to cases of disease and physical abnormalities. Mental traits are much more difficult to study, because they are more difficult to recognize with certainty, and not unfrequently two observers would differ in their opinion as to whether a certain trait was or was not present. I have been able to construct two large pedigrees, one showing the inheritance of artistic, and the other of musical ability. Both pedigrees are so remarkable that they appeared to me to be well worthy of publication. They are large, fairly complete, and throw some light on the mode of inheritance. In both cases my informants have been the judges as to whether the various members of the families are to be classed as artistic or musical, but I shall give all the particulars of each individual as far as they have been gathered, in order that readers may form their own opinion as to the way they should be classified. I think the known facts accord with the classification shown in the charts, where the black circles indicate those members who are artistic in the one case, and musical in the other, and the white circles those who do not possess these traits.

Artistic ability.

In this chart the black circles indicate the artistic members of the family: the white circles the non-artistic. All the artistic members are stated to be *skilful* in drawing: most of them also show marked

ability in painting, and several excel in design.   In addition to ability in drawing, they show the following particulars:—

Generation I.

No. 2 is "very artistic."

Generation II.

No.   1.   Paints original pictures and designs.
No.   2.   Teacher of drawing: art critic.
No.   5.   Draws well.
(No.   6.   Does not draw: clever actress.)
No. 12.   Architect, and builder of most beautiful houses.
No. 13.   Paints pictures.
No. 14.   Paints: designs art embroidery.   (Husband: a school master.)

Generation III.

No.   1.   Designer and actress: highly artistic.
No.   2.   Surgeon.
No.   3.   Surgeon.
No.   4.   Surgeon: artistic photographer: has invented some improvements in photography.
No.   5.   Artistic and belongs to an artistic family: her father is a theological author.
No.   9.   Clever actress: lady doctor.
Nos. 11, 12 and 13 are accomplished musicians.
No. 16.   Paints: accomplished musician.
No. 18.   Paints: accomplished musician: has several certificates for drawing.
No. 20.   Paints: accomplished musician.
No. 21.   Designs art needlework and embroidery.
No. 23.   Designs and makes stained glass windows.
No. 24.   Draws in black and white: teacher of drawing.
No. 25.   Skilful table decorator: horticulturist.
No. 26.   Paints pictures.
No. 27.   Designer by profession.
No. 30.   Artist by profession.   Has pictures in the House of Lords and the Royal Exchange.
No. 31.   Designer by profession.
No. 32.   Artist by profession: formerly designer at Waring's.

No. 34.   Designs and makes art needlework.

No. 36.   Designs and makes art needlework.

Generation IV.

Nos. 1 and 2.   Paint.

No. 10.   Draws portraits.

The following members of the family are "exceptionally gifted" as artists:

II.   Nos. 1 and 13.

III.   Nos. 23, 30, and 32.

IV.   No. 10.

Most of those in Generation IV are still young, and their talent is not fully developed.

No. 12 in Generation II seems to have been a strange individual. He always declined to speak about his relatives, or to say who they were. He would give no particulars of his early life. He predicted that he would die on a certain day: a week before its arrival he took to his bed, and died on the specified day.

Is the inheritance in this family such as one expects from a Mendelian point of view?

Marked general ability has been stated to be inherited as a Mendelian recessive.

If artistic ability is recessive, what are the expectations from various matings?

They are as follows:—

(1)   Two non-artistic parents, if pure dominants, should have non-artistic children only.

In Generation II, no. 4 and his wife have no artistic ability, and have five children, all of whom resemble the parents.

The same result is seen in the children of the twin sister of no. 8.

In Generation III the only child of no. 15 is not artistic.

These results are perfectly in accord with the theory that artistic ability is a recessive.

(2)   Where an artistic individual marries one who is not artistic but has artistic relatives (and if heterozygous in this respect), the expectation is for the children to be of both types in approximately equal numbers.

The actual results are:

$$\text{I.} \quad 1+2 \quad = \frac{3 \text{ artistic}}{2 \text{ non-artistic}}$$

$$\text{II.} \quad 5+6 \quad = \frac{2}{3}$$

$$7+8 \quad = \frac{3}{3}$$

$$9+10 \quad = \frac{3}{3}$$

$$\text{III.} \quad 17+17a = \frac{3}{2}$$

$$\Bigg\} = \frac{14 \text{ artistic}}{13 \text{ not artistic}}$$

Here again the result is strictly Mendelian.

(3) If both parents are artistic *all* the children will be artistic. Two recessives breed true to the recessive character, and do not re-produce the dominant type.

The chart shows that in six cases both parents are artistic. The number of children in each family is respectively as follows: 4, 11, 2, 2, 2 and 3. The last four families are in the youngest generation, and are still children. The numbers will probably be increased considerably. In these six families there are twenty-four children, twenty-three of whom are artistic, and one (III, 28) is of uncertain type. The result here is strictly Mendelian.

The chart contains sixty-four artistic members, by far the largest artistic family of which I have been able to collect particulars. In nineteen instances both parents are shown.

Twins have appeared four times, in each instance being of the same sex. Two pairs are artistic and two are not.

The above particulars have been collected for me, with great care, by the lady $\frac{11}{a}$ in Generation III. She is personally acquainted with most of her relatives, and those she does not know she has received information of, by correspondence, and verbal inquiries extending over a period of about nine months. She is a highly educated lady, and an accomplished musician, but has no knowledge of Mendel's Laws, or of theories of inheritance which might bias her in forming an opinion. She does not know what is to be expected from any particular type of parentage. I wish to express to her my most sincere thanks for all the trouble she has taken, but am not at liberty to mention her by name.

As already stated the black circles indicate those members of the family who are "skilful in drawing," but skill in drawing does not comprise the whole of artistic ability. In its full development artistic ability seems to me to comprise at least five distinct talents: namely

1. Perception of form.
2. Perception of colour.
3. Memory of form.
4. Memory of colour.
5. Inventiveness. (Design.)

Those who possess nos. 1 and 2 may be able to make excellent copies: but could not draw things from memory—they may have no *clear* remembrance of form or colour.

Those who possess nos. 3 and 4 must of necessity have 1 and 2 also.

A person may have all the first four, and be totally lacking in inventive faculty.

Anyone who possesses no. 5 must of necessity possess all the others; so that this must be regarded as the highest form of artistic ability. This family is interesting from this point of view. Several members are stated to be skilful as designers, which means that they possess the inventive faculty.

Nothing can now be stated as to whether there were any designers in Generation I. There are two in Generation II (nos. 1 and 12).

In Generation III there are twelve designers, and they are all children of the two mentioned in Generation II: two of them are the children of II, 1, and ten are the children of II, 12.

If design is inherited like drawing ability, then II, 14 was probably a designer, but if so the fact has not been mentioned. It will be interesting to notice whether "design" develops in the children in the fourth generation. It is noteworthy that no other artistic member of the third generation is talented in this way beyond those mentioned: in other words, only those who design have children who show the same talent.

Musical ability.

This chart shows the pedigree of a family of organists. The musical members are indicated by black circles, the non-musical by white ones.

By musical ability is here meant something more than mere ability to play certain musical instruments. It implies the possession of the musical Sense, whatever that is. I am informed by a professional

PEDIGREE OF FAMILY OF ORGANISTS.

The figures in brackets [ ] give the number of children who either died young or whose musical tastes are unknown.

♂ = musical male.
♂ = unmusical male.
♀ = musical female.
♀ = unmusical female.
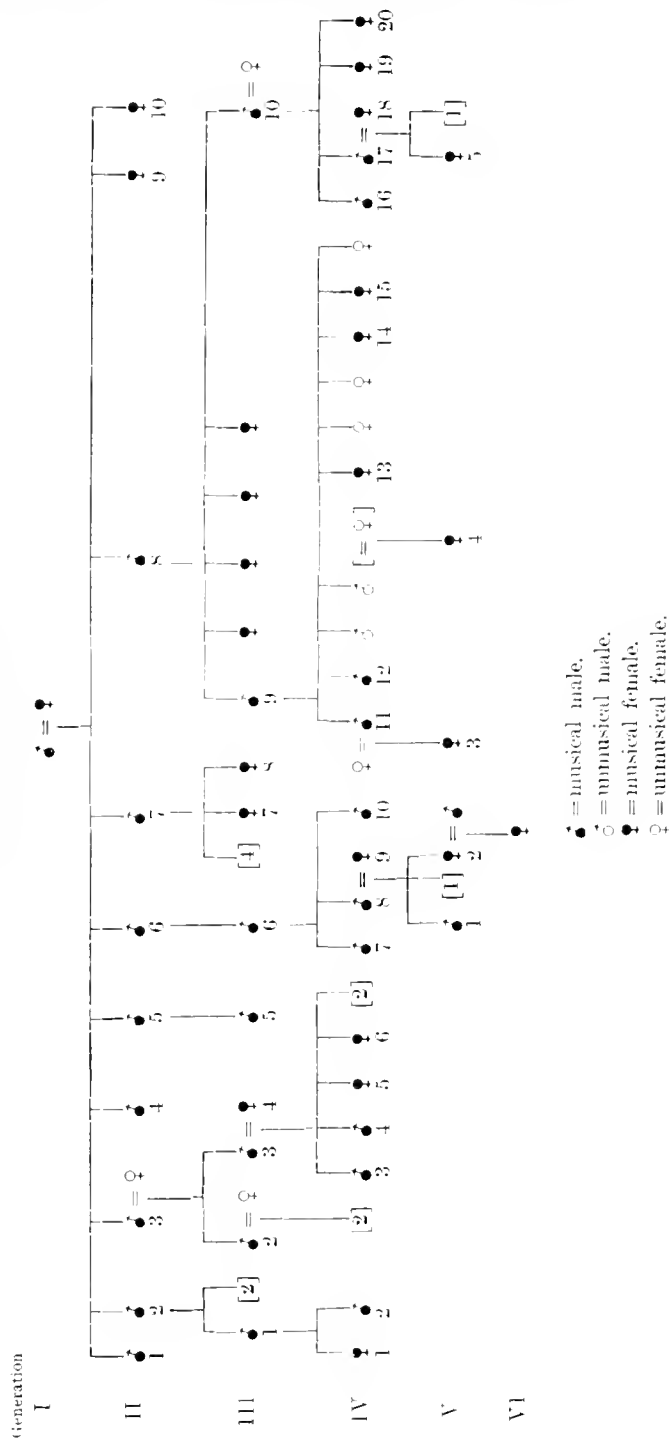
musician, who has had large experience as a conductor, that there are many performers on brass instruments who cannot be considered really musical; and it is certainly true that the pianoforte is often played in a mechanical sort of way by people quite devoid of musical tastes.

I have asked several eminent professional teachers for a definition of the term "musical," and so far have not received a satisfactory answer.

It appears to me, however, that a man must be considered "musical" if he is capable of acting as professional organist and choir master, and especially if he holds his post for forty years or more, as several members of this family have done. It would appear indeed that such a post must demand the possession of musical talent of a high order.

Moreover, several members of this family are mentioned in the *British Musical Biography* (1897).

The chart at first sight looks fairly complete, but the expert in Mendelian records will observe omissions that are to be regretted. There is an absence of *one* of the parents in six instances, so that one cannot tell precisely how many children should show musical talent on theoretical grounds. On the other hand both parents are shown in ten instances, but even here, unfortunately, it is not known whether the non-musical parent ($\female$ or $\male$) has a musical ancestry or not.

Despite these defects the chart is of great interest as showing that musical ability is, in some way, markedly hereditary; and the chart is complete in so far as the children of each parental pair is concerned, and the type of each is known with the exception of the few shown in brackets [ ].

Hurst[1] asserts that the musical sense is inherited as a Mendelian 'recessive.'

If that is correct, we should expect the same results of the various matings that are indicated under (1), (2) and (3) in the case of artistic ability, so that only the actual results in this musical family need be mentioned.

(1) Two non-musical parents.

There is only one instance in this family: viz. the parents of no. 4 in Generation V.

One of the parents, the father, belongs to this musical family, but nothing is known of the ancestry of the mother. If she also belonged to a musical family, both she and her husband may be heterozygous

[1] "Mendel's Law of Heredity and its application to Man," *Leicester Lit. and Phil. Soc. Trans.* XII. 1908, p. 35.

(*DR*) as to musical capacity, and might therefore have musical children, but only one in every four according to theory. If three more children are born they should not be musical.

So that the appearance of V, 4 is unexpected, but is not certainly contrary to the theory that musical ability is recessive.

(2) Where one parent is musical and the other not, but with musical ancestry.

In this case 50 per cent. of the children may be musical, but a larger percentage is not expected.

In III, 9 we get five musical, and five not musical : this is exactly in accord with the above statement.

In II, 3 and III, 10 all the children are musical, and some of them are said to be especially talented. These cases do not accord with the theory that musical ability is inherited as a simple Mendelian recessive, for there are far too many musical members.

(3) If both parents are musical all the children should be so.

Generation II is a striking corroboration of the theory in this respect : it is seen that all the ten children of the couple shown in Generation I were musical. The same is true of the children of III, 3 and 4, IV, 8 and 9, 17 and 18, V, 2, so far as they can be traced. Of twenty-two children, the type of eighteen is known, and they are without exception musical. Nothing is known of the other four children, not even the sex.

The results here are therefore perfectly in accord with Mendelian theory.

With regard to those mentioned in the last paragraph under (2), where the musical members are present in apparent excess, it will be observed that the un-musical parent is in every case the mother. The father was a professional musician holding an important appointment. His musical status would altogether overshadow and eclipse that of his wife, even if she were musical, and one can imagine that any musical talent she possessed might thus be overlooked. The wife moreover is so much engaged with household duties that she has little time for "accomplishments."

If one were able to state that these mothers were "musical" with the talent undeveloped, then one would expect all the children to be musical. Moreover my informant only considers those individuals "musical" who were "performers." Yet there is little doubt that the musical sense may be present without the person learning to play on a musical instrument.

I do not suggest that these considerations will explain the actual results observed in this family, but I do maintain that they are points which should be taken into account.

The following are the particulars I have been able to gather respecting the individual members. Except in one instance V, 2, the inheritance has occurred through the male members of the family, the females having in the great majority of instances remained single.

Generation I.

No. 1. This was John Simms, the earliest member of the family now traceable. He was an organist. He had a musical wife. They had ten children, every one of whom had musical ability of a high order.

Generation II.

No. 1. Bishop Simms, organist at the Church of St Philip, Birmingham (now the Cathedral Church), for about forty years.

No. 2. James, organist at Bromsgrove Church for forty-four years, and also at Chaddesley, Worcester.

No. 3. Samuel, organist at St Thomas's Church, Stourbridge, for fifty years. He was one of the finest players of the time. He died sometime before 1860. His wife "belonged to a musical family."

No. 4. Henry, organist at a church near Stourbridge.

No. 5. Jesse, organist at the parish church of Handsworth.

No. 6. Edward, organist at Ashbourne, Derbyshire.

No. 7. George Frederick, "held musical appointments."

No. 8. Francis or Frank, musical, but not a professional organist.

Nos. 9 and 10 were musical.

Generation III.

No. 1. John Simms, succeeded his father as organist. He had two brothers, one of whom died young: the other was "chef" to the Duke of Fife and "was probably not musical." Nothing is known about the mother.

No. 2. Arthur, organist. He married Miss Shore of Wrexham, who was not musical.

He was born in 1839 at Birmingham. In 1874 obtained the degree of Mus. Bac., Oxford: 1875–80, organist St Mary's Cathedral, Glasgow: then for seven years organist and choir master at Forest School, Walthamstow: afterwards at Chard and Hythe. The obituary notice in the *Church Times* describes him as "a Saint."

No. 3. Samuel, succeeded his father as organist. Later he was organist at Ladywood (St John's), Birmingham, and afterwards at St Cyprian's, Haymills, Birmingham. He married Miss Davies, a cousin, who was musical. Of their six children four are known to be musical, the other two are untraceable.

No. 5. Henry, born 1804, organist; succeeded his uncle Bishop at St Philip's. Between them they occupied the organ stool for about eighty years. He was famous as an extempore player and as a teacher of pianoforte and singing. He died May 1st, 1872.

No. 6. Edward, born at Oldswinford, Worcestershire, February 10th, 1800, organist successively at Holy Trinity and St John Baptist Churches, Coventry, then for fifty-eight years (1828–86) at St Michael's. He resigned at the age of 86. He established the Coventry Choral Society, and had many distinguished pupils, including George Eliot. It is to him that reference is made in *Middlemarch*. He died in 1893.

Nos. 7 and 8 are "moderately accomplished musicians."

No. 9. Henry, organist at Oldswinford Church, Stourbridge, for forty-two years. Died aged 70.

No. 10. Frank, has played church services since 14 years of age, and is now 83. Has held three church appointments as organist. He has supplied me with most of the information about his family, and his estimate as to musical ability of the various members is here recorded. His wife "belonged to a musical family."

He had four sisters, Elizabeth, Emma, Frances and Mira, all musical.

Generation IV.

Nos. 1 and 2 "are both musical."

No. 3. Samuel, succeeded his father as organist at St Cyprian's, Haymills, Birmingham, where he remained for over thirty years.

No. 4. Arthur, is a Bachelor of Music.

Nos. 5 and 6 "are very musical."

No. 7. Robert Henry, born at Birmingham in 1829, was organist for a short time (1853–56) at Wrexham Parish Church, but died young, suddenly, "as the bells were ringing for morning service."

No. 8. Edward Bishop, organist at Wrexham Parish Church for about forty years (1856–94). He married Miss Shore who was very musical. He died at Wrexham in 1913.

No. 10. George Handel, "was full of music." Became curate of Stoke Prior Church, near Bromsgrove, and later vicar of Haymills, Birmingham.

Nos. 11 and 12. Frank and James Herbert; one studied under Dr Arnold of Winchester Cathedral, and the other at Wells Cathedral. Both obtained first-class musical appointments (Professorships) in the United States. "Frank's wife was not of a musical family, but she was a clever literary writer."

No. 13. Anne, musical.

Nos. 14 and 15. Mary and Emily, were both musical.

No. 16. Henry, was for some time organist at Gresford. Later he entered the medical profession. He and

No. 17. Alfred are " full of the blood of the old ones." Alfred later took to law.

No. 18. Wife of Alfred, is clever musically.

No. 19. Kate }
No. 20. Clara } are both musical performers.

Generation V.

No. 1. Musical.

No. 2. "Among the best."

No. 3. Music teacher by profession, "is exceedingly clever." She is "a public performer."
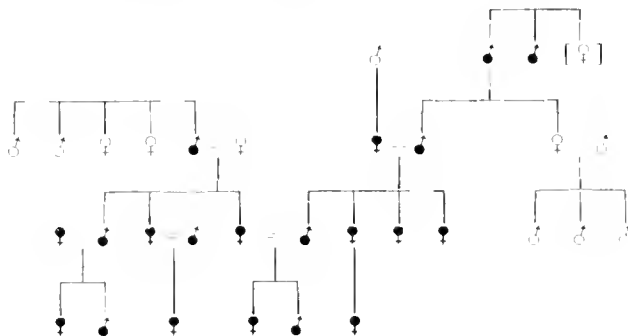
Nos. 4 and 5 are very gifted.

Generation VI.

No. 1 is very gifted.

I am able to give the pedigrees of four other musical families. In the E. D. and to a less extent in the R. family the ability is of a very
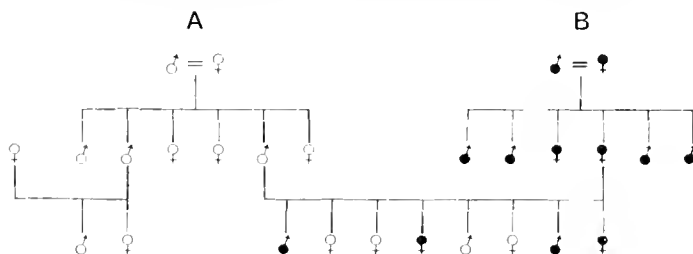
INHERITANCE OF MUSICAL ABILITY. R. Family.

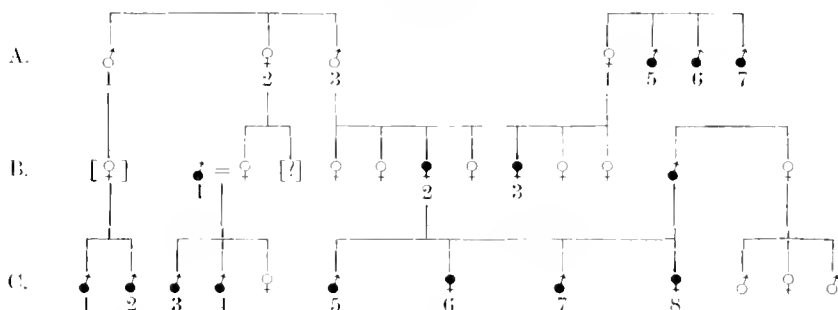It agrees with the theory that where both parents are musical all the children should be musical.

INHERITANCE OF MUSICAL ABILITY. S. D. Family.

A.   Both parents non-musical have only non-musical children.

B.   Both parents musical : all the children are musical.

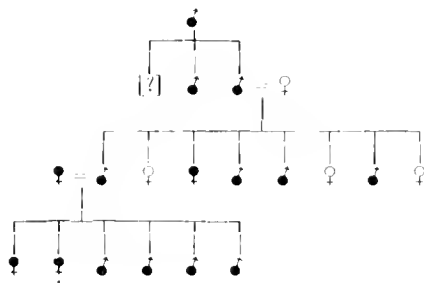A   B

INHERITANCE OF MUSICAL ABILITY IN VERY HIGH
DEGREE. E. D. Family.

A 6, C 1, 2, 3 and 4 are professional musicians with university
degrees.

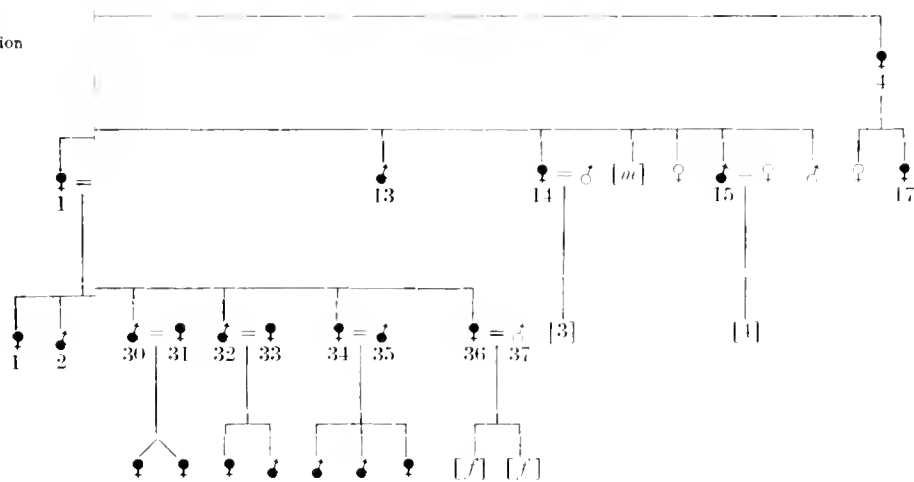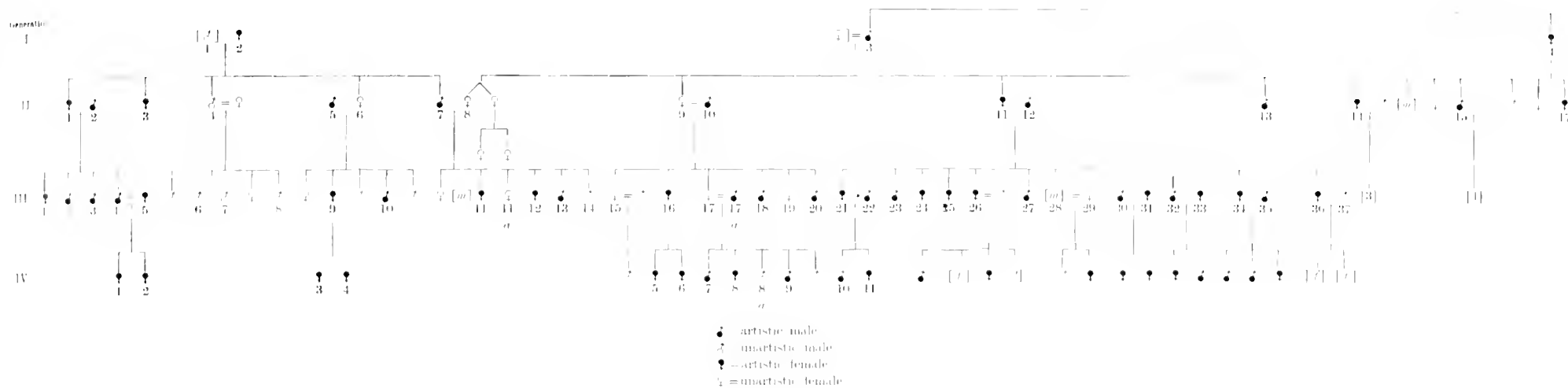INHERITANCE OF MUSICAL ABILITY. J. Family.

type.

Generation

CHART SHOWING INHERITANCE OF ARTISTIC ABILITY

The type of those in brackets [ ] either died very young or are of unknown or uncertain type

high order ; many of the members are professionals, and have university degrees in music. In every case they show that where both parents are musical all the children show musical ability. The E. D. and the J. families agree with the theory that musical talent is inherited as an ordinary recessive, like dwarfness in *Pisum sativum*. In the R. pedigree the three children of ♂ = ♀ are all musical and this is exceptional.

The chart of the S. D. family shows two branches (or roots). One A contains non-musical members exclusively : the B branch is entirely musical. When both parents are musical all the children are musical (B). Where musical ability is lacking in both parents, all the children lack musical ability (A). The two families became united by marriage. According to Mendelian theory — i.e. supposing musical ability to be transmitted as an ordinary recessive—the children should all lack musical ability, but as a matter of fact exactly 50 per cent. are musical, and two of them are professionals of great ability. The inheritance is exactly what would be looked for if the father (♂) were heterozygous, but from the pedigree he is more probably homozygous.

The conclusions that one must come to from a study of these pedigrees are

(1) The inheritance is strictly Mendelian where both parents show the 'recessive' trait.

(2) There are too many musical children born, when only one parent (apparently) is musical.

(3) No satisfactory explanation can be offered for the latter feature.

(4) Musical sense is probably recessive.

COLOUR AND PATTERN-TRANSFERENCE IN PHEASANT CROSSES.

By ROSE HAIG THOMAS, F.Z.S., F.L.S.

CONTENTS.

FOREWORD.

An apology is needed for the somewhat voluminous number of instances that accompany this paper of the various methods of pattern-transference; but gathering these from notes and observations carried on over eight or nine years, the experimentalist must inevitably lay before the reader a vast amount of detail, though it is imperative that this shall be presented in as condensed a form as is compatible with brevity and lucidity. The indulgence of the reader is asked if the result has failed to meet these requirements.

An account of the independent inheritance of the moult habit in hybrids seems inseparable from the discussion of plumage, and some observations on the correlation of plumage and call note it is hoped may be thought of interest.

INTRODUCTION.

Throughout the course of all these pheasant-hybridising experiments pattern-transference has been a notable feature, and though in the earlier crosses some instances escaped observation, yet the preservation of all the skins of every cross, ringed, numbered, lettered and labelled in cabinets has rendered their detection a simple matter. In all previous papers[1] mention has been made of these phenomena, but in each case space forbad a complete description of the numerous instances observed; now so many facts have been collected that the time has come to assemble and present certain of them together. The following order will be maintained as closely as possible in their grouping and arrangement.

1st. Transmission of pattern, colour, structure and form of the female of his species by the male parent to his female offspring.

2nd. Transmission of pattern, colour, structure and form of the male of her species by the female parent to her male offspring.

3rd. Pattern and colour-transference transmitted by the male parent to the female offspring.

4th. Pattern and colour-transference transmitted by the female parent to the male offspring.

These will be traced first in the sterile hybrids, secondly in the fertile hybrids.

FERTILE HYBRIDS.

However absorbing may be the study of sterile hybrids to the breeder, that of the fertile hybrids is still more attractive, for the problem of the stability of each new pattern as it arises is of unending interest. In experiment expectation is often followed by realisation which stimulates endeavour and fires the imagination with an ardent and unfailing enthusiasm.

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[1] "On some Skins of Hybrid Pheasants," Rose Haig Thomas, *Proc. Zool. Soc.* April, 1910; "On Experimental Pheasant Breeding," Rose Haig Thomas, *Proc. Zool. Soc.* March, 1911; "Experimental Pheasant Breeding," Rose Haig Thomas, *Proc. Zool. Soc.* Sept. 1912; "On Sterile and Hybrid Pheasants," Geoffrey Smith and Rose Haig Thomas, *Journal of Genetics*, June, 1913.

Reversing the history of the sweet pea, pheasant varieties seem to arise rather by the gain of or transposition of factors than by the loss of them, except where arrested immature plumage takes the place of adult plumage. Such pheasant hybrids then may be said to have lost the factor for complete adult plumage, but this arrested development has ever been accompanied by sterility.

Examining inherited mutations one can see that this inheritance is governed by Mendel's law. Had it been possible in No. 1 Series to have bred from all individuals of F_3 instead of only the two most marked mutations, more might have been added to our knowledge of one way of evolution.

The expectation with the few numbers inevitable in pheasant-breeding is that the dominant would of necessity be forced on the breeder, but the results do not show this to be the case. Segregation is sharp and distinct even in the day old chick, whose down forecasts which parent species when adult it will most or altogether resemble.

CHARACTERS OF PARENT SPECIES.

The colour, size, habit and patterned or unpatterned condition of the natural species used in the series of crosses dealt with in this paper are briefly described.

Gennaeus nycthemerus (Silver) ♂. Large bird, broad build.
        Colours black and white.
        Superior plumage *patterned*.
        Inferior plumage *unpatterned*.
        Legs rose colour.
        Habit bold, friendly to man.

Gennaeus nycthemerus ♀. Large bird, broad build.
        Colours olive grey, black and white.
        Superior plumage *unpatterned*.
        Inferior plumage *patterned*.
        Legs scarlet.
        Habit bold, friendly to man.

Gennaeus swinhoei (Swinhoe) ♂. Bird smaller than Silver, slenderer build.
        Colours metallic blue, green, and copper, white and black.
        Superior plumage *patterned*.
        Inferior plumage *unpatterned*.
        Legs dark red.
        Habit shy, seeking concealment.

Gennaeus swinhoei ♀.   Bird smaller than Silver, slenderer build.
    Colours buff brown, rufous black.
    Superior plumage *patterned*.
    Inferior plumage *patterned*.
    Legs dark red.
    Habit shy, seeking concealment.

Phasianus formosanus (Formosan) ♂.   Bird large, very light colour.
    Colours buff, grey, metallic copper, ruby and green, collar *white*.
    Superior plumage *patterned*.
    Inferior plumage *patterned*
    Structure of posterior back feathers and tail coverts *degenerate*.
    Legs pale grey.
    Habit tame, temperament calm.

Phasianus formosanus ♀.   Bird large, very light colour.
    Superior plumage *patterned*.
    Inferior plumage buff *unpatterned*.
    Legs pale grey.
    Habit tame, temperament calm.

Phasianus versicolor (Versicolor) ♂.   Bird small, very dark colour.
    Colours metallic green and ruby, grey, black, *white absent*.
    Superior plumage *patterned*.
    Inferior plumage *unpatterned*.
    Legs dark grey.
    Habit very wild and nervous.
    Structure of posterior, back feathers and tail coverts *degenerate*.

Phasianus versicolor ♀.   Bird small, very dark.
    Superior plumage *patterned*.
    Inferior plumage *patterned*.
    Legs dark grey.
    Habit very wild and nervous.

Phasianus reevesi (Reeves) ♂.   Bird very large.
    Colours golden buff, much white, every feather margined with
      metallic copper or black.
    Superior plumage *patterned*.
    Inferior plumage *patterned*.
    Structure of posterior back feathers and tail coverts *normal*.
    Legs grey.
    Habit bold, combative.

Phasianus reevesi ♀. Bird large.

  Colours cream, brown, black, white.

  Superior plumage *patterned* (bold design).

  Inferior plumage *patterned* (bold design).

  Legs pinkish grey.

It may be of interest to describe the difference between a normal and a degenerate feather. The normal feather consists of the following parts: quill, rachis, right vane, left vane, barbs, barbules and hooklets.

The down feather has the same first five parts but the barbules are small and the hooklets absent.

The degenerate feather has the first five parts but both barbules and hooklets are absent.

The schemes of mating were as follows:

Sterile Hybrids.

Series "A."

1906   *Gennaeus swinhoei* ♀ × *Phasianus reevesi* ♂

mated 1907, 1908   *Phasianus reevesi* ♀ × F_1 ♂, all eggs infertile

Series "B."

1909   *Phasianus reevesi* ♀ × *Phasianus versicolor* ♂

F_1.   3 ♀   5 ♂

1910, 1911, 1912, mated *inter se*, with parent stock, and in open pen with common pheasant, all sterile. No eggs laid, no mating observed.

Series "C."

1910   *Phasianus reevesi* × *Phasianus formosanus*

F_1.   (2) ♀   (2) ♂

1911 F_1.   ♀ ♂, mated *inter se*.

    F_1.   ♀, mated with male parent species. Both sterile, no mating observed, no eggs laid.

1912   Two F_1.   ♀, mated with F_1 ♂ *inter se* sterile, no mating, no eggs.

The scheme of matings for the series of fertile hybrids is given on

PEDIGREE OF FERTILE HYBRIDS.
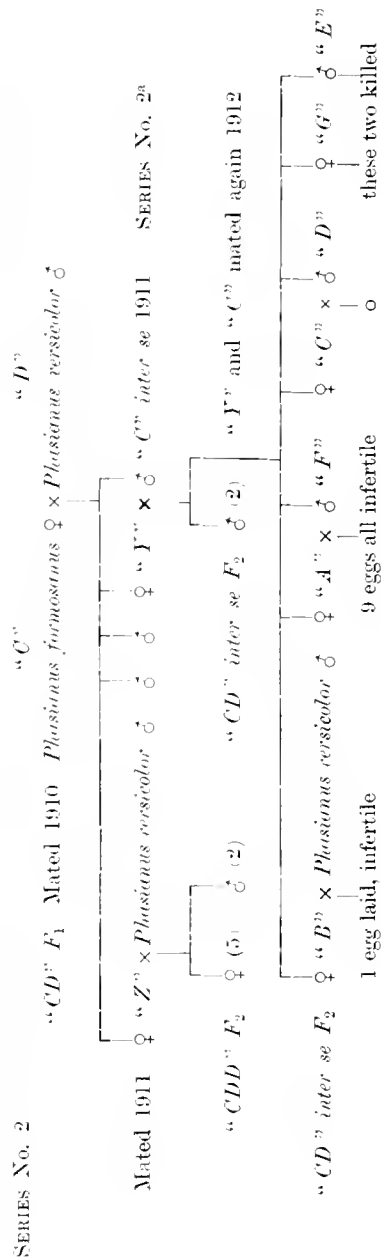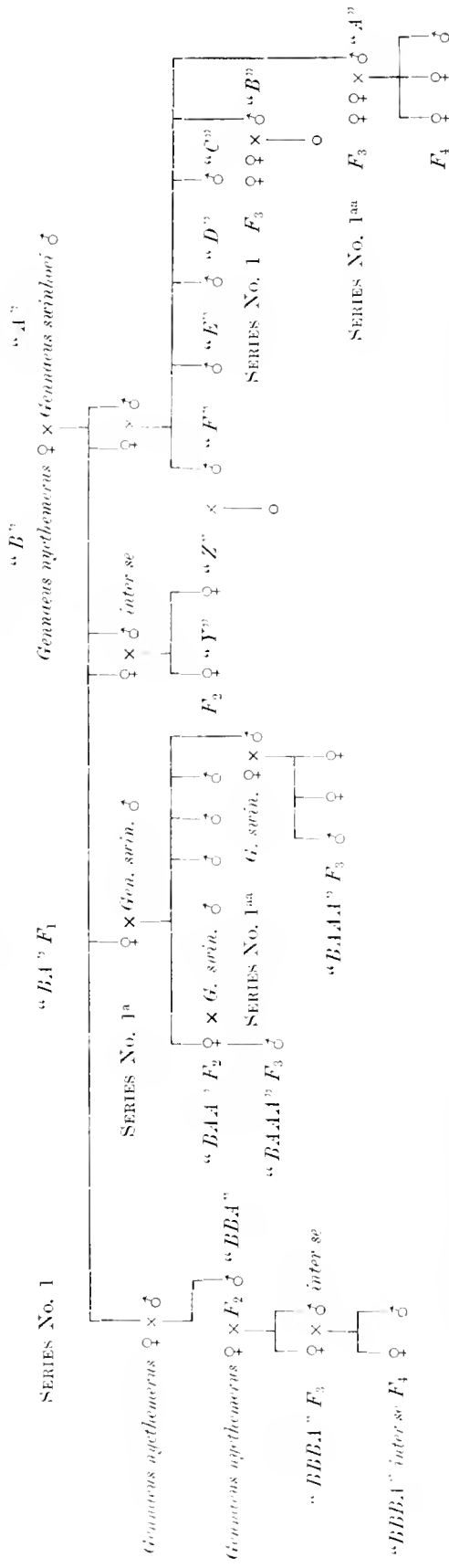
TRANSFERENCE OF PLUMAGE PATTERNS.

The first point to be remarked in connection with our subject is the simple transmission of the female plumage of his species by the male parent to his female offspring, an unexpected sex-limitation, and also the same simple transmission of the male plumage of her species by the female parent to her male offspring.

Closer observation reveals more intricate forms of inheritance which are designated as pattern and colour-transferences, both male and female parents transmitting pattern and colour from one plumage area in their species to a different area in their male and female offspring, some of which have proved to be mutations fixed and heritable.

In one singular case the female parent transmitted a pattern from one area in her own plumage to another in her male descendant, also transmitting to the same individual (F_2 *inter se* ♂) the plumage of the male of her species but reversed, a light pattern on a dark ground instead of a dark pattern on a light ground. This bird proved infertile the only season he was mated, so the heritable qualities of his strange plumage could not be tested.

Another mutation arose through the female parent transmitting pattern and colour from one area in the transition plumage of the young male of her species to another area in her female offspring[1], in this case the bird proved fertile and the mutation was shown to be heritable[2]. It is generally admitted that in a wild condition pheasant species cross as easily as they do in captivity, and where such crosses are fertile these phenomena of pattern and colour transferences would be a simple explanation of the numerous closely allied species and varieties found in the somewhat limited area of their habitat. Even the varying patterns so remarkable in the female Silver pheasant (*Gennaeus nycthemerus*) might be explained by crosses occurring between the Silver and Swinhoe species, owing to the possible flight of the latter from the Island of Formosa to the mainland opposite, and such a flight would not be less possible than that of grouse which ringed on the Island of Rum have been shot on a Yorkshire moor.

All cross-breeding experiments produce disturbance of pattern and colour in the central rectrices, one frequent change is the transference to the central rectrices of a lateral rectrix pattern or colour. The following cases illustrate this remark.

[1] Series 1, F_3.
[2] *Journal of Genetics*, Vol. III. No. 4. April, 1914.

The pattern of the Silver ♀ 3rd laterals was found on the *centrals* of the immature plumage of her F_1 male offspring aged ten months, also on her F_1 female offspring's adult centrals, and on the centrals of her descendant F_2 *inter se* ♂ " *B*."

An instance of double colour-transference in this area was noted: the black colour of the laterals of a male parent (Swinhoe ♂), was found transferred to the centrals of a male descendant F_2 Si. × Sw. × Sw. (Series 1ᵃᵃ in pedigree, fertile hybrids), while the white of the central rectrices of the male Swinhoe was transferred to one lateral on the same bird.

A case of the abnormal in a pure species was observed, a *Ph. formosanus* female, who was seen to combine abnormality of behaviour, treading the other females and uttering the male challenge, with an assumption of male plumage and pendulous wattles.

Among the fertile hybrids, the first of the three series of the Silver Swinhoe crosses 1, 1ᵃ and 1ᵃᵃ in pedigree engages attention, for in Series 1 two plumage mutations arose, one in the male, the other in the female line, and that the two, though dissimilar in colour and pattern, were intimately connected, is attested by the coloration of the immature plumage in both sexes, the male and female mutation showing similar differences at that stage from the more normal individuals of the same cross and generation. The chief mutation consisted in the males of a change in the areas of throat, breast, flank and thigh tuft from the unpatterned condition found in the males of both parent species to a patterned condition not present in either in the same areas, the origin of which in the first three areas can be traced to the marginal and central interscapulars of *Gen. swinhoei* the male parent of F_1 " *BA*," and in the fourth area to the female Swinhoe breast and flank patterns. The colour mutation was the occurrence of much white mingled with the black common to both male parent species in these four areas, whilst in the first three areas there was also a change of form to an extremely pointed type of feather and a degeneration in the dimension of the feathers: these three mutations occur in F_1 " *BA*," F_2 " *BBA*," F_3 " *BBBA* " and F_4 " *BBBA* " *inter se*. The first and simplest form of the new colour and pattern is a white rachis, in other examples the white invades both vanes, forming a stripe down the feather, in some widening at the tip, in others widening at the base, some feathers, more particularly in the throat area, have the outer ends altogether white, like the Swinhoe central interscapular ; other variations of the mutation occur, one recalling the breast pattern of the female of the male parent

species, the other suggesting the breast pattern of the female parent of
the three generations, but the general effect on the living bird when
seen near is a striped pattern, and when seen in the distance this melts
into a grey effect very different from the non-protective coloration of
the inferior parts of the males of both parent species.

Amongst the males of Series I in pedigree another mutation has
been observed, namely in the primaries. *Gen. nyc.* ♂ primaries have
a white ground with 19 or 20 waving bands of black, which in some
feathers are zigzag, the rachis is grey at the quill end, changing to
white towards the outer end. *Gen. swinhoei* ♂ has an unpatterned
black primary and the rachis black. F_1 "*BA*" are hybrid in colour and
pattern with the black rachis of Swinhoe throughout the length of the
feather, and this black rachis remains constant and the same in F_2 "*BBA*,"
F_3 "*BBBA*" and F_4 "*BBBA*" *inter se* with one exception In these
three generations, F_2, F_3 and F_4, the primaries have the waving bands
of *Gen. nyc.* on white ground but these bands are diminished in numbers
in some birds, or broken up into patches or into dots and dashes in others,
the colour is changed from black to grey, whilst the white area is largely
increased. To instance the reduction in number of bands from the pure
Silver type of 20, a glance at Plate XLVIII, fig. "*Z*" shows these
reduced to 6, whilst in Plate XLVIII, "*Y*," and in Plate XLVII, "*C*"
and "*Q*" are good examples of the breaking up into dots and dashes
with a vastly increased white area. This mutation of the wing is found
correlated with that of the other three mutated areas. In the throat,
breast and flank mutations a few birds in F_1 "*BA*," F_2 "*BBA*" and F_3
"*BBBA*" generations showed segregation back to the black feathers of
the males of both parent species in one or other area, but on only one
bird in all four generations was the male Silver pattern found on the
primaries.

Life History of Sterile Hybrids.

Proceeding in the order indicated, the life history of the sterile
hybrids will be sketched.

Reeves × Versicolor, 1909.

In this cross infertility was considerable, out of a total of 63 eggs
39 were infertile, the average of deaths on hatching was not so great,
6 out of 14, and in this cross as in every other, whether sterile or fertile,
the sex ratio showed an excess of males over females, for out of

13 hatched, 10 were males and there was only one dead in shell, whose sex was not determined. Here as in other accounts a slight discrepancy between the results and the egg numbers is due to an occasional egg being broken by the hens in the nests, and forgotten to be noted: however these eggs never had birds in them, and might always have been reckoned infertile.

At ten days old F_1 Reeves × Versicolor chicks developed an abnormal wildness, rapidly rushing up and down their little run and dashing their heads against the wire netting. Four days later fighting of a desperate character took place. In the first hatch two birds fought and eventually slew one another, force had to be used to separate them in the first instance, but the true nature of this death struggle was not recognised at first, and being again left together the fight recommenced and ended fatally: both chicks on dissection proved to be males. In the second hatch four chicks fought at 11 days old, one was slain: this bird also was a male.

In the third hatch two birds fought at 18 days old, one lingered six days and then died of the injuries received: this chick also was a male, and had tiny sharp spurs, a precocious development of a secondary sexual character. In every case the attack was made with the bill on the head, and dissection of the dead suggested that it was the males that fought.

Abnormal behaviour in the females commenced at the age of two months, when a female F_1 Reeves × Versicolor fought a male F_1 Reeves × Versicolor so savagely and persistently that she had to be removed to a separate pen.

In 1910 three pairs of F_1 Reeves × Versicolor were mated *inter se*, no mating was observed, no eggs were laid, all three pairs were sterile.

During the mating season of 1911, two of the female F_1 Reeves × Versicolor fought at daybreak, one was found dead, though still warm at 6 a.m., the other had a bleeding head. The season suggested rivalry, possibly the breeding instinct existed in these sterile hybrids, arousing that jealousy which has so often in spring occasioned tragedies in my pheasantry. Three trials were made in the season of 1911, the first, another *inter se* mating between a pair of F_1 Reeves × Versicolor with the same result as in 1910, complete sterility, the second a mating with female F_1 Reeves × Versicolor and a *Ph. versicolor* ♂, the male parent species, no eggs were laid: the third, two male F_1 Reeves × Versicolor with wings cut were placed in a large open pen to run with the common pheasant hens, no mating was ever observed, nor was there ever any

fighting between these two hybrids and the common male pheasant running in the same open pen, neither was there any sign of a cross in any of the chicks raised, upwards of a thousand. The absence of rivalry here suggests absolute sterility. During the breeding season of 1912 several of these birds were sent to Mr Geoffrey Smith for cytological investigation, the results of his researches were published in the *Journal of Genetics*, Vol. III. No. 1, June, 1913, showing great abnormalities and degeneration in the sexual organs.

Reeves × *Formosan*, 1910.

In 1910, *Ph. reevesi* ♀ the bold combative species was crossed with *Ph. formosanus* ♂ a species of tame calm nature. Infertility of the eggs was great, of 36 laid there were 28 infertile, 8 chicks were hatched, 4 died, all males. Of the 4 reared, 2 were males, 2 females, the sex ratio again showing the preponderance of males. In this cross strange wild behaviour began at 10 days of age and at 17 days 4 of the chicks fought in a mêlée, three succumbed, which on dissection proved to be males.

From these observations and the previous evidence of the other sterile hybrids the Reeves-Versicolor cross, it is plain that all the combatants were males, which is the more astonishing as in the adult stage we find the males so peaceable and friendly together even in the breeding season, whereas the females, though peaceable as chicks were so aggressive to one another as adults that they had to be separated.
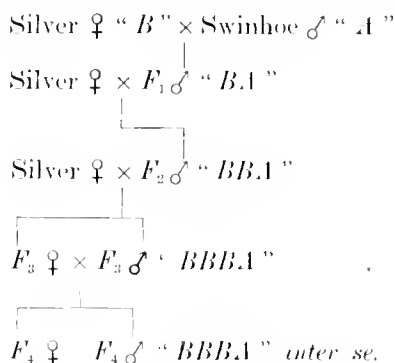
In 1911 F_1 *reevesi* × *formosanus* ♀ was mated with the male parent species *Ph. formosanus* ♂, she laid no eggs.

The same season a pair of F_1 *reevesi* × *formosanus* were mated *inter se*, no eggs were laid, no mating observed.

In 1912 F_1 *Ph. reevesi* × *formosanus* were again mated *inter se*, no mating was seen, no eggs were laid.

The precocious combativeness of the males in early chickhood followed by such perfect friendliness in the adult stage even in the mating season, and the reverse conditions observed in the females, their abnormal dimensions, being nearly as big bodied as the males, and the assumption of male plumage suggested some intricate interchange of condition in the sexual organs. Three of these birds also were examined by Mr Geoffrey Smith, whose interesting account of their abnormal sexual condition may be seen in Vol. III. No. 1 of the *Journal of Genetics*, June, 1913.

Life History of Series 1 Fertile Hybrids.

Silver ♀ " B " × Swinhoe ♂ " A "

Silver ♀ × F_1 ♂ " BA "

Silver ♀ × F_2 ♂ " BBA "

F_3 ♀ × F_3 ♂ " $BBBA$ "

F_4 ♀ F_4 ♂ " $BBBA$ " *inter se.*

In the scheme of mating for Series 1 in pedigree *Fertile Hybrids* a cross was made between a Silver female and a Swinhoe male and continued between the Silver female and F_1 male, and again between the Silver female and F_2 male, F_3 being mated *inter se* to produce F_4 (page 248). An account of the female offspring of this series has already been published[1], in which it was shown that in spite of the three doses of Silver to one of Swinhoe, the females remained, to a certain extent, hybrid in all four generations, and that pattern and colour-transference produced mutations amongst them which proved heritable and were governed by Mendel's law. The males in this series also exhibit mutations to a marked degree, and as was the case with the females, these have been ascertained in most instances to arise from pattern and colour-transferences from one area to another, some originating from both sexes of the male parent species, others from changes occurring in characters derived from the *male* of the *female* parent species, and these mutations also proved heritable, and gave evidence of Mendelian segregation.

It is a curious fact that the adult leg-colour of both males and females of these four generations of Series 1, was the leg-colour of the males of the female parent species. The Silver hen did not, even after three crosses, transmit the colour of her own legs, scarlet, to her female offspring, but transmitted to them the leg-colour of the male of her species.

[1] *Journal of Genetics*, Vol. III. April, 1914, "The Transmission of Secondary Characters in Pheasants," Rose Haig Thomas.

The number of plumage mutations in the males of Series 1 recorded in this paper are six: throat, breast, flank, thigh tuft, primary and central rectrix, the five first transmitted through four generations, the sixth appearing first in F_2. Their description in detail will be found in the Appendix.

To fully appreciate the importance of these fixed mutations in four of these areas of the males of Series 1, we must refer to the description of the males of the two species crossed. We find in both of them that all the inferior parts are *unpatterned*, yet we get a fixed *patterned* condition of the inferior parts in F_2 "BBA," F_3 "$BBBA$" and F_4 "$BBBA$" *inter se* with a certain segregation showing that the unpatterned condition has become recessive.

Taking the four areas of the inferior parts—throat, breast, flank, thigh tuft separately, and making the reckoning from three generations, we find the segregation in them is as follows, F_2 "BBA," F_3 "$BBBA$" and F_4 "$BBBA$" *inter se*, eighteen males.

		Mutation	
		Present	Absent
Males: F_2 "BBA," 5; F_3 "$BBBA$," 8; F_4 "$BBBA$" *inter se*, 5.			
Source of mutation, male Swinhoe interscapulars	Throat	14	4
	Breast	12	6
	Flank	13	5
Source of mutation, female Swinhoe breast and flank	Thigh-tuft	16	2
	Totals ...	55	17

The fifth mutation in the males of Series 1 was the central rectrices which in F_1 "BA," F_2 "BBA" is found heavily patterned, while in F_3 "$BBBA$" and F_4 "$BBBA$" *inter se* Mendelian segregation occurs, one individual having the absolute male Swinhoe type central rectrix which is unpatterned white with white rachis.

In this fifth area a *patterned* takes the place of an *unpatterned* condition, as in the first four mutations.

In the sixth area, the primaries, two changes occur—a marked reduction in the number of bands, and the breaking up of these into dots and dashes, with proportionate increase of the white area; here the tendency is for pattern to disappear rather than to increase.

It should be emphatically stated that in Series 1 male mutations throat, breast, and flank, the pattern does not in the remotest degree resemble the transitional plumage patterns found in two of those areas on the young male Silver: therefore arrested development cannot explain the phenomena. The origin is clearly traced to the male

parent of the first generation F_1 " BA " (Swinhoe) and is a pattern-transference of fixed and heritable nature.

After research had revealed the origin of the mutation patterns in Series 1 on throat, breast, and flank to be derived from the marginal interscapulars of the male Swinhoe, a very interesting confirmation of this was found in Series 1^a in the pedigree F_2 " BAA " which have the same mutations in the same areas, but having also the male Swinhoe interscapular patch, the simple descent was easily traced from its source in beautiful sequence. The thigh tuft mutation was a transmission of the *vandyke* pattern from the breast and flank of the female Swinhoe not from the transitional breast pattern of the immature male Silver which is a *rounded* design.

Throat, breast, flank and thigh tuft feathers were extracted from the female Swinhoe, the immature male Silver and Series 1 males F_1 " BA," F_2 " BBA," F_3 " $BBBA$ " and F_4 " $BBBA$ " *inter se*, also the interscapulars from the male Swinhoe, and were laid side by side; after a minute and careful examination and comparison, no doubt whatever existed as to the sources of these four mutations.

Thus we see pattern-transference maintaining a hybrid condition, forming mutations fixed, constant, and capable of transmission through these four generations of males, phenomena identical with those of the females in the same series, previously recorded.

Wattles.

Professor R. C. Punnett wrote asking for information as to the behaviour of this character in the Silver Swinhoe cross (Series 1 in pedigree); on consulting the records some notes were found on the size, colour, and hair punctuation of the face skin or wattle. In 1909 the increased size of the wattles in F_2 " BBA " Series 1 was recorded with the remark that large "face skin" was a Silver character. After Professor Punnett drew attention to the wattles I made examination in the mating season of 1914, accompanied by rough drawings of the differences in size of wattle in the following three birds: male Swinhoe, male Silver, male F_4 " $BBBA$ " *inter se* Series 1. The wattles of the Swinhoe are considerably smaller than those of the Silver, but the wattles of F_4 Series 1 in pedigree are much larger than those of the Silver, the growth is prolonged upwards over the head, meeting above the bill in one solid mass somewhat ridged in the centre. The male Silver has always a division of black crest feathers between the two
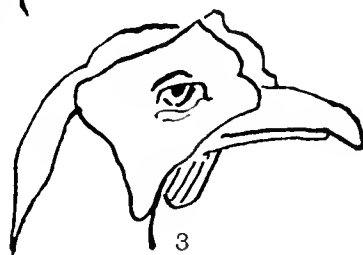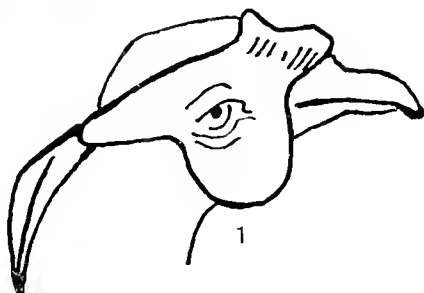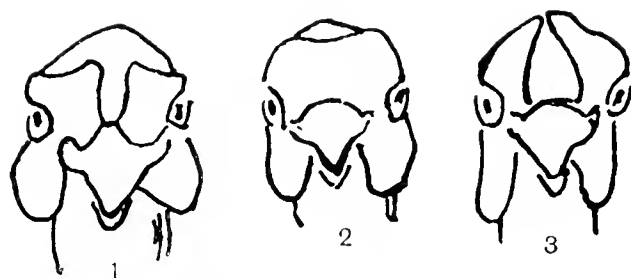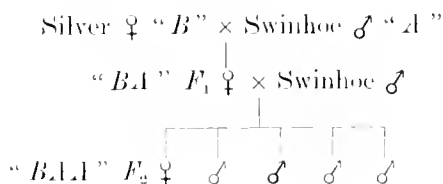
1. Male Silver.
2. Male F_4 (Silver × Swinhoe) " E."
3. Male Swinhoe.

wattles and on the Swinhoe this division is still wider. The fact that a median "comb" can arise as the result of a cross between two forms in which it is not present is not without interest in connection with the origin of the comb in *Gallus*.

The examination showed the wattles of F_4 to be a seventh mutation in Series 1 males and that the character was derived from the female parent.

LIFE HISTORY OF SERIES 1ᵃ FERTILE HYBRIDS.

Series 1ᵃ.

Silver ♀ " B " × Swinhoe ♂ " A "

" BA " F_1 ♀ × Swinhoe ♂

" BAA " F_2 ♀   ♂   ♂   ♂   ♂

In Series 1ᵃ of the pedigree the mating was reversed. F_1 " BA " Silver × Swinhoe female was mated with the male parent and bred in F_2 " BAA," a female so closely resembling the female of the male parent species that the phenomenon was described in a short paper and the birds exhibited to the Zoological Society[1], as being an occurrence both unexpected and not previously recorded. This F_2 " BAA " female mated with a Swinhoe male, bred an F_3 " $BAAA$ " male not to be distinguished from a pure male Swinhoe. The skins of these birds were presented to the Cambridge Museum of Zoology in 1910, where they may be seen. This curious experience of the transmission of the female plumage and dimension of the female of his species by the male parent to his female offspring in Series 1ᵃ of the pedigree led to making further trial with the same scheme of mating between two varieties of a different species: a *Phasianus formosanus* female was crossed with a *Phasianus versicolor* male (page 248) named Series 2 in the pedigree, with the expectation that the phenomenon would be repeated; the result verified that expectation, and an account of the experiment, with illustrations, was published by the Zoological Society in 1912[2] in which it was shown that not only the pattern and the colour

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[1] *Proc. Zool. Soc.* 1910, "On some Skins of Hybrid Pheasants," Rose Haig Thomas.

[2] *Proc. Zool. Soc.* 1912, "Experimental Pheasant Breeding," Rose Haig Thomas; *Proc. Zool. Soc.* 1912, "On Eggs of Pheasants," Rose Haig Thomas.

of the female of his species, but also the moral qualities and the size of the egg, were transmitted by the male parent to his female offspring.

Three experiments of *inter se* mating have been made, one with Thaumalea, one with Gennaeus, one with Phasianus; some of the results of one have been published[1], but further trials have been undertaken to test the results recorded in that paper, which are not yet completed. The other two *inter se* crosses, *Gennaeus nyc. × Gennaeus swinhoei*, and *Ph. formosanus × Ph. versicolor* furnish a great number of cases of pattern and colour transmission which will not be dealt with here. A separate paper on these *inter se* experiments is contemplated later on.

Of the four brothers of F_2 "*BAA*" extracted female Swinhoe (*P. Z. S.* 1910, pp. 884–885), one only F_2 "*BAA*" male, "*D*" was used to breed with; the quarrelsome tempers of F_2 "*BAA*" males, "*A*," "*B*" and "*C*," which necessitated separation, never abated, even after the mating season was ended; two of these three males F_2 "*A*" and F_2 "*B*" were especially interesting; though the plumage was very dark and Swinhoe in coloration it was hybrid, but the point of importance was the discovery that both had the Series 1 mutation on breast and flank, and the manner of its occurrence was further proof of the source of that mutation. In these two birds the mutation begins at the junction of the interscapulars, which are Swinhoe type, with the marginal anterior breast feathers leading directly on to the centre breast and flank. The marginal feathers commence with a broad pattern like the interscapulars, the pattern gradually narrowing as the mutation extends and spreads over the centre of the breast, and creeps down the flanks. The derivation was thus traced in all stages in the clearest manner through a perfect series of pattern gradations, confirming the theory previously held of the origin of the Series 1 breast and flank mutation. The other "*BAA*" F_2 male "*C*" was a nearly pure type Swinhoe, but the back feathers were margined with burnished copper like the scapulars in place of blue lustre like the type; also in the tail the centrals showed both colour and pattern-transference, being rufous with a black pattern like the female Swinhoe laterals; this case of transference *was* a transmission by the *male* parent to his *male* offspring of the *female* characters of his species.

*Series 1*ˢᵗ *in the pedigree.* F_2 "*BAA*" male "*D*" was a pure type Swinhoe; the records note that no difference could be distinguished in any character between this bird and a male Swinhoe in the next

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[1] *Proc. Zool. Soc.* 1911, "On Experimental Pheasant Breeding," Rose Haig Thomas.

pen : later a comparison of the two skins showed that some minor distinctions existed. For instance, the interscapular patch on F_2 "BAA" male "D" looked a less solid white mass than that of the type due to the white portion of each interscapular being less, and the black portion larger, giving a slightly chequered appearance ; also, the blue lustre margin on the tail coverts is a little narrower in the extracted Swinhoe than in the type, and on one or two of the tail coverts some fulvous mottling on the black ground was noticed. But such differences are trifling and probably exist on different individuals of the male Swinhoes. This "BAA" F_2 male "D" was mated with two pure female Swinhoes, and his offspring F_3 "$BAAA$," two females and one male, were Swinhoe : the male (F_3 ♂ "B"), however, though Swinhoe in every character, had a double colour-transference in the tail, the centrals being *black* instead of *white*, and one of the laterals *white* instead of *black*.

The two female F_3 were mated with a bird from the *inter se* Series 1ᵇ of the pedigree F_2 *inter se* male "A" extracted Swinhoe, and the offspring produced, F_4, two females and one male, were again pure Swinhoe in every character, without any mutation.

All the males of Series 1ᵃ and 1ᵃᵃ of the pedigree had one factor transmitted from the Silver, namely, the moult, which was early, instead of late like the Swinhoe, and the method also was Silver, an interesting independent segregation ; the three F_4 of Series 1ᵃᵃ formed, however, an exception to this rule, for all three birds had the Swinhoe moult, both period and method. All the females of Series 1ᵃᵃ F_3 and F_4 had the pattern somewhat more mottled than the type, but as considerable individual variations in pattern and colour are discernible amongst individuals of the pure Swinhoe race, these slight deflections from type are not regarded as reflecting a hybrid condition.

Nature and Inheritance of Moult.

Parent Species and Series 1, 1ᵃ, 1ᵃᵃ *and* 1ᵇ *of the pedigree.*

			Period	Method, tail
"B."	Gen. *nycthemerus*	male	Early	Centrals before laterals
"	"	female	"	" "
"A."	Gen. *swinhoei*	male	Late	Laterals before centrals
"	"	female	"	" "

In the Swinhoe the centrals only commence growth after the laterals have grown to their full length.

In Series 1 F_1 "BA," F_2 "BBA," F_3 "$BBBA$" and F_4 "$BBBA$" *inter se* the moult, both period and method, is Silver.

In this Series it is recorded that dimension, call, habit, plumage and moult are correlated.

In Series 1^a F_3 "$BAAA$" male (offspring of extracted Swinhoe female, exhibited and described, *P. Z. S.* 1909, pp. 884–885) segregation occurred, for though a perfect Swinhoe in dimension, call, plumage and habit, this bird had the moult period and method of the Silver species, and a similar independent moult segregation was observed in the males of Series 1^{aa}, with the exception of the male and female F_4 (offspring of F_3 female in Series 1^{aa}, crossed with F_2 *inter se* "A" male in Series 1^b), where no moult segregation occurred, plumage, dimension, call, habit and moult period and method were all Swinhoe.

There is a sex difference in the moult of the Silver species, the male starting the moult two months before the female. This difference is found in *Phasianus* also, but though many records of both male and female Swinhoe moult were made, I have not any special records of the Swinhoe moult sex difference, but it is probably the same.

The hybrid males of the Silver Swinhoe cross Series 1 of the pedigree have a double moult, the first in spring and early summer, the second in September: this double moult I have sometimes thought might be due to inheritance of both male and female moult habit, but there must be some other factor at work, for no matter in what month in the year the hybrids are picked up, there are loose feathers that fall out and quills of young feathers growing in; the hybridising of pheasants seems to create a moult disturbance and confusion, even in the fourth generation. Amongst the records it is noted on Nov. 4 that a Silver male (*Gen. nycthemerus*) in fine plumage arrived and was killed for the museum, the moult was complete, no loose feathers fell out, nor was the plumage anywhere interrupted with the quills of new feathers as would have been found on the bodies of any of the hybrid pheasants of whatsoever cross, for the constant state of semi-moult is a character common to all these crosses, with the extracted Swinhoe exceptions above mentioned. The condition is not a mere sex mosaic or racial mosaic but rather a mutation mosaic.

Fertile Hybrids.

Parent species:

			Period	Method
"C."	*Phasianus formosanus*	male	Early	Rapid
,,	,,	female	,,	,,
"D."	*Phasianus versicolor*	male	Late	Slow
,,	,,	female	,,	,,

Series 2 in the pedigree.

In *P.Z.S.* 1912, pp. 542–543, was published an observation of peculiar interest relating to moult and plumage in the crest area of the three F_1 "*CD*" males of this cross which I have the kind permission of the Zoological Society to re-state here.

The centre crest feathers were dark.

Colour	Versicolor

They were fully developed.

Early rapid moult	Formosanus

The marginal feathers were pale.

Colour	Formosanus

They were undeveloped, many still in the quill.

Late slow moult	Versicolor

Thus we see in one area the independent segregation of four factors. An examination of the males of both parent species was made at the same time, showing Formosanus to have a fully developed crest and that of Versicolor to be undeveloped, mostly still in the quill.

Series 2^a in the pedigree.

The moult of F_2 *inter se* Formosanus × Versicolor followed the plumage, an extracted Versicolor female moulted late and slow, an extracted Formosanus female moulted early.

HABITS.

The habit of the sterile hybrids has been already remarked upon in their life history. The following notes concern the parent species and fertile hybrids.

Parent Species of Series 1, 1^a *and* 1^{aa} *in the pedigree.*

			Habit
"*B.*"	*Gen. nycthemerus*	male	Bold, tame, noisy
	,,	,, female	Bold, tame, silent
"*A.*"	*Gen. swinhoei*	male	Shy, quiet, instinct for concealment
	,,	,, female	,, ,, ,,

Series 1.

(F_1 " *BA*," F_2 " *BBA* " and F_3 " *BBBA* " males bred back with female Silver.)

F_2 " *BBA* " males passed the breeding season of 1909 in one pen together in undisturbed friendship, these friendly relations were not due to immaturity, for a brother F_2 " *BBA*," also a 1908 bird, was mated with Silver females and bred a large number of offspring in the same season. In 1910 and 1911, F_3 " *BBBA* " males also lived together in perfect harmony and undisturbed friendship through both breeding seasons. In 1912, F_4 " *BBBA* " *inter se* males passed the breeding season together amicably, although only separated by a wire netting from F_4 " *BBBA* " *inter se* females, but on the 10th July, after the mating season was over, four of the cocks fought the fifth by turns, when one left off another began; the poor bird was finally rescued, dirty, draggled, half plucked, still screaming with pain and fright.

The F_2 " *BBA* " and F_3 " *BBBA* " and F_4 " *BBBA* " *inter se* females had been just as friendly as the males, penned together through 1909, 1910, 1911 and 1912, until the 10th May, 1912, when four F_4 " *BBBA* " *inter se* females fought the fifth, which had to be removed. Curious to relate, both birds selected for persecution had been previously selected to breed together as the most prominent mutations. (The female laid eggs in the seasons of 1913 and 1914 but they were all infertile, though the male showed every sign of breeding in both seasons.)

Series 1^a *in the pedigree   and   Series* 1^{aa} *in the pedigree.*

Females F_1 and F_2 bred back with male Swinhoe	Female F_1 bred back with male Swinhoe
	Male F_2 bred back with female Swinhoe
	Female F_3 bred back with male F_2 *inter se* " *A* "

Three F_2 "BAA" males (1^a) were dreadfully quarrelsome birds, fought desperately and had always to be kept penned apart in or out of the breeding season; all three had Swinhoe plumage of somewhat hybrid arrangement, the fourth "BAA" male was Swinhoe in every character and mated with a female Swinhoe produced two F_3 "$BAAA$" females and a male ("B") all Swinhoe in plumage, dimension and call; the F_3 "$BAAA$" male "B" had playful ways worthy of notice; when the pen was approached the bird lowered its head, made short quick runs, then rapid turns back to the same spot with a nimble grace pretty to witness, simulating a pretended fear and semi-antagonism towards the observer. In sharp distinction to this bird was F_2 "BBA" male Series 1, a very noisy bird, like all male Silvers he never ceased his aggressive chatter till the observer moved on, whereas F_3 "$BAAA$" male "B," although taking great notice of his visitor with the above described antics, was generally a silent bird; sometimes, however, he emitted a sound like a low growl accompanied by a vertical jerking of the tail. The pure male Swinhoe and the two extracted Swinhoe males, Series 1^a of the pedigree F_3 "$BAAA$" and Series 1^{aa} of the pedigree F_4 exhibited exactly the same curious habit of lowering the head, accompanied by a muttered growl and vertical jerkings of the tail, so that these wary, watchful, queer ways and altered demeanour, marking an interest in man, were a purely Swinhoe habit and were correlated with the plumage: many records are found during September noting the sideways skip, the lowered head, and the growl in extracted and pure Swinhoe males. It was noted that the females of both parent species were generally characterless as were also the extracted Silver females, Series 1, and extracted Swinhoe females, Series 1^a and 1^{aa}; though when confined together in a pen without a male they have been occasionally observed running after one another in a sort of play, none had any really playful habits, or were either friendly or otherwise with man; all were dull and uninteresting, with the single exception of one bird in Series 1^b of the pedigree, a female F_2 *inter se*, whose ways will be described in another paper. Notes are frequent on the shy habit of the Swinhoe and on the bold manner of the Silver, whether of pure or extracted race, and all tend to show that unlike the moult factor, which seems to segregate independently, in most crosses habit and plumage are correlated.

Series 2 in the pedigree.

In the Formosan-Versicolor cross (*P. Z. S.* 1912, pp. 540-542) the wild nervous temperament is transmitted to his F_1 "*CD*" and F_2 "*CDD*" female offspring by the male Versicolor, and amongst the F_2 *inter se* Series 2^a, Versicolor temperament is found correlated with Versicolor plumage and Formosanus temperament coupled with Formosanus plumage. In this cross the records of habit in the youngest chicks show the same coupling, the darkest down being allied to the more nervous, the palest down to the bolder temperament. It may here be mentioned that when nest-dry the chicks are graded light, medium, dark, with white, red or black thread tied round the leg, the threads being cut off and renewed as the leg grows, until the bird is six weeks old, of age to be ringed, thus the colour and habit are traced from birth. In the chick stage dimension also was linked with colour and habit, the darkest chicks were the smallest (Versicolor) and those with the palest down the largest (Formosanus). In Series 2 the colour of the iris was observed and proved to be another character of the female of his race transmitted by the male parent to his female offspring[1].

Challenge or Call.

Conversational Voice.

Gen. nycthemerus ♂ }	Challenge a low note
Gen. nycthemerus ♀ }	Conversational voice high tone
Gen. swinhoei ♂ }	Challenge a high note: 4 or 5 tones higher than the male Silver
Gen. swinhoei ♀ }	Conversational voice, a low mutter

Series 1, 1^a and 1^{aa} records establish the fact that plumage, dimension and call in the adult birds are invariably correlated, and that habit and

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[1] Since writing "The Transmission of Secondary Sexual Characters in Pheasants," published April, 1914, in *Journal of Genetics*, Vol. III., I had occasion to examine the crest of an immature male Silver passing through the transition to the adult plumage, most of the feathers were black as the adult, but amongst them was one which resembled the male Swinhoe adult crest in structure and form and was of a brown colour mottled with fulvous resembling in fact one or two of the "*A*" series female crests which had been pronounced hybrid; now if the crest of the immature male Silver had been examined earlier it is possible that more of these feathers might have been found. In any case the discovery of this feather modifies the presumption that F_2, F_3 and F_4 female crests were hybrid, and might indicate that the mutation in the crests was due to pattern-transference by the female parent to her female offspring of the male transitional plumage of her species.

call were also associated. Hybrid birds of Swinhoe type have the Swinhoe challenge and voice, hybrid birds of Silver type have the Silver challenge and voice.

A habit of visiting the pheasantry every morning at six o'clock has rendered the task of recording the varying calls an easy one, and as hybrids and pure races are, though separately penned, all in the same field there is ample opportunity for comparison.

INHERITANCE OF LEG CHARACTERS.

Legs.

Gen. nycthemerus ♂		*Gen. swinhoei* ♂	
Dimension	Thick	Dimension	Thin
Colour	Rose	Colour	Dark red
Spur	Thick, curved	Spur	Slender, straight
Gen. nycthemerus ♀		*Gen. swinhoei* ♀	
Dimension	Thick	Dimension	Thin
Colour	Scarlet	Colour	Dark red

Series 1 *in the pedigree,* " *BBA*," " *BBBA*," " *BBBA* " *inter se.*

All males exact to Silver type.

Transmitted by female parent.

Series 1ᵃ *and* 1ᵃᵃ *in the pedigree,* " *BAA*," " *BAAA*," " *BAAAA*."

Males and females exact to Swinhoe type.

SUMMARY.

1. The more the data of these experiments in pheasant cross breeding are examined the clearer and more certain becomes the conviction that they proceed on definite lines, subject to some fixed law, certain experiments repeated have shown that the male parent always transmits the female characters of his species to his female offspring and the female parent transmits to her male offspring many of the male characters of her species. The female parent has likewise transmitted the male characters of her species to her female offspring in one or two areas, and in many areas in the case of male-assuming female offspring (sterile hybrids).

2. The phenomena of pattern and colour-transference is present in all the experiments made in pheasant crosses up to date. These have been observed to consist sometimes of transference from one area to a different area in the same sex, or from one area to a different area in the opposite sex, or from an area in one sex to the same area in the opposite sex.

3. In three crosses these pattern and colour-transferences have been accompanied by sterility, in each of the three sterile crosses *Phasianus reevesi* has been one of the parents, twice with other varieties of *Phasianus*, and once with *Gennaeus*.

4. These pattern and colour-transferences are the cause in the fertile hybrids of mutations, discontinuous and heritable, changes so marked, that if occurring from natural hybridisation between species they would undoubtedly be labelled varieties by the systematist. In some cases they are associated with degeneration of dimension in the feathers.

5. In the fertile hybrids, plumage, dimension, leg colour, and structure, habit, call, are all correlated, but moult is independent and liable to great disturbance in hybridisation.

6. The question of dominance in the Silver Swinhoe crosses (fertile hybrids) remains in doubt. For whilst in Series 1, Swinhoe seems eliminated after a second dose of female Silver, we find in Series 1^a that Silver is apparently eliminated after the second dose of male Swinhoe, And though in Series 1 the origin of several areas of discontinuous mutation are directly traced to pattern-transference from the Swinhoe, yet on the other hand some of the hybrid plumage in Series 1^a of the three male F_2 "BAA" under examination will probably be found to be due to Silver pattern-transference. Of that there is little doubt.

The contemplated paper on the *inter se* experiments in this cross may throw light on the subject, but records and observations do not encourage this belief: however research may modify that impression.

APPENDIX A.

Sterile Hybrids.

Transmission by male parent to female offspring of the female plumage of his species.

F_1.   Reeves ♀ × Versicolor ♂, ♀ "*B*."   1909 bird: (1909 plumage). Geoffrey Smith examined and made preparations of sexual organs.

Breast:	Centre, dull buff.
Pattern-transference.	Anterior, patterned like female Versicolor posterior.
Flanks:	Patterned, transmitted by male parent.
Back:	Structure ⎫ Form ⎪ female Versicolor, transmitted by male Colour ⎬ parent. (Pl. XXXV, fig. 9.) Pattern ⎭
Interscapulars:	Form ⎫ female Versicolor with some modifications Pattern⎬ towards male Reeves, transmitted by both ⎭ parents. (Pl. XXXVII, figs. 9, 10.)
Scapulars:	Pattern, female Versicolor, transmitted by male parent. (Pl. XXXVI, fig. 10.)

Wing:	Primary and coverts ⎫
	   matching ⎪ female Versicolor, transmitted
	Secondary and coverts ⎬ by male parent.
	   matching ⎭

Tail:	Centrals ⎫ all rectrices similar in pattern, male Reeves Laterals ⎬ character, also female Versicolor character. Pattern, hybrid, transmitted by both parents.
Tail covert:	Pattern, female Versicolor, transmitted by male parent. (Pl. XXXIV, fig. 7.)

Nearly every character of this hen was transmitted by the male parent. In every instance the transmission of character by either parent was of the opposite sex of their species.

F_1.   Reeves ♀ × Formosan ♂, ♀ "*B*."   1910 bird.   Geoffrey Smith (" *B* ").

Breast:	Colour, female Formosan, a slightly deeper buff, the flank pattern of female Formosan appears on the

anterior breast in a very faint staining. Extracted buff feathers show the pattern high up on the shaft; the buff of the next feather overlies this, hiding the pattern, and gives the appearance of a self buff breast, transmitted by *male* parent.

Wing: Primary }
Secondary } hybrid, transmitted by both parents.

Primary group, major coverts, }
  female Formosan } transmitted by *male*
Secondary group, major coverts, } parent.
  female Formosan }

Interscapulars: Pattern female Formosan, slight modification towards male Reeves, transmitted by both parents. (Pl. XXXVIII, figs. 11, 12.)

Scapulars: Female Formosan, transmitted by *male* parent. (Pl. XXXVI, fig. 8.)

Back: Form }
Colour } female Formosan, transmitted by *male* parent.
Pattern } (Pl. XXXV, fig. 7.)

Tail: Hybrid, transmitted by both parents. (Pl. XXXIV, fig. 8; Pl. XXXIX, fig. 7.)

Female plumage, 1910, similar to ♀ " *B.*"

F_1. Reeves ♀ × Formosan ♂, ♀ " *Y.*" 1910 bird: (1911 plumage). Geoffrey Smith made cytological examinations and preparations.

Male-assuming, 1911, 1912.

Head: Male Reeves, transmitted by female parent. Bird's plumage much injured by method of killing.

Breast: Male Reeves with variation.

Wing: *Primary*, female Formosan pattern: colour, hybrid. *Secondary*, pattern; colour, hybrid.

Interscapulars:
  Pattern-
  transference. *Anterior*, male Reeves posterior, transmitted by female parent.
  Posterior, hybrid, some female Formosan pattern.

Tail: *Centrals*, pattern male Reeves in miniature, transmitted by female parent.
  Laterals, centrals and laterals all one pattern, transmitted by female parent. (Pl. XXXIV, fig. 9.)

Note. The 1910 plumage of F_1 Reeves × Formosan ♀ " *Y*" was female Formosan, transmitted by male parent: the male plumage assumed in 1911 and 1912 was that of the male Reeves transmitted by the female parent.

These secondary sexual characters were developed just before the first mating season at the age of ten months.

Transmission by female parent to male offspring of the male plumage of her species.

F_1.   Reeves ♀ × Versicolor ♂, ♂ " *A*." 1909 bird: Geoffrey Smith examined sexual organs and made preparations from them.

Notes, October 27th, 1912.

Head :	Pattern, male Reeves.
	Cheeks, white, transmitted by female parent.
	Crest, white, extending to a broken white collar; intervening spaces a dull black.
Bill :	Finch form, Reeves, transmitted by female parent.
Body :	Particularly on back and breast tinged all over with a beautiful purple lustre found on male Versicolor
Colour-transference.	throat, but the green lustre so conspicuous in the male Versicolor plumage is absent, transmitted by male parent.

Back : (Pl. XXXV, fig. 4.)

Anterior feathers.

Structure, male Reeves, transmitted by female parent.

Form   hybrid ⎫
Colour ⎫   ⎬ nearer male Versicolor.
Pattern ⎭ hybrid ⎭

Posterior feathers.

Structure, male Reeves ⎫
Form,   female Reeves ⎭ transmitted by female parent.

Colour ⎫
Pattern ⎭ hybrid nearer male Versicolor.

Wing :	Primary, male Reeves, transmitted by female parent.
	Secondary, male Reeves, only the fawn patch on the outer vane is longer and narrower and the white is absent.
Scapulars :	Pattern strongly resembles male Reeves, but is hybrid. (Pl. XXXVI, fig 9.)

Interscapulars: (Pl. XXXVII, figs. 11, 12.) Pattern, colour, female Versicolor.

Tail: Length, 1 foot, 11 inches (male Reeves tail, 3 to 4 feet; male Versicolor tail, 1 foot).

Centrals } all of one pattern (a male Reeves character,
Laterals } also female Versicolor character).

Structure } are female Reeves, wide bands dark, narrow
Pattern } bands light.

Colour, hybrid, a rich red brown, a colour found on female Reeves laterals and on male Reeves centrals.

Tail Coverts: Structure, male Reeves (normal), transmitted by female parent. (Pl. XXXIV, fig. 10.)

Form, female Reeves.

Colour } hybrid.
Pattern }

F_1.   Reeves ♀ × Formosan ♂. ♂.   1910 bird.

Head }
Neck } Male Reeves, a replica of pattern and colouring of male
Eyeskin } Reeves, white and dull black with the exception of the throat, which is dull black instead of white, transmitted by female parent.

Breast: Form, male Reeves, transmitted by female parent.

Pattern } hybrid.
Colour }

Interscapulars: Form, pattern, male Reeves, transmitted by female parent.

Colour of margin, burnished copper, male Formosan breast. (Pl. XXXVIII, figs. 9, 10.)

Scapulars: Hybrid, rich colouring. (Pl. XXXVI, fig. 7.)

Wing: Primary, pattern } male Reeves, transmitted by female
     colour } parent.

Secondary, hybrid.

Wing Coverts: Major, median and minor, mutations, not found in any area of Reeves ♂ ♀ or Formosan ♂ ♀.

Back: (Pl. XXXV, fig. 2.)

     Anterior.

     Structure } male Reeves, transmitted by female parent.
     Form }

     Colour, hybrid, male Reeves, male Formosan, very rich and varied.

Posterior.

Structure, male Reeves, transmitted by female parent.

Form
Colour } hybrid but nearer male Reeves.
Pattern

Tail :   Length, 2 feet (male Reeves 3 or 4 feet, Formosan about 1 foot).

Centrals } alike in pattern, transmitted by female
Laterals } parent, male Reeves. (Pl. XXXIX, fig. 3.)
Colour, wide black bands divided by narrow bright brown hybrid bands, pale brown margins.

Tail Coverts :   Structure, male Reeves, transmitted by female parent.

Form
Colour } hybrid nearer male Reeves. (Pl. XXXIV,
Pattern }   fig. 4.)

Colour-transference.

Male parent to *male* offspring.

Colour-transference. F_1.   Reeves × Formosan ♂.

Interscapulars : Margin of feathers colour of male Formosan *breast.*
Back :   Purple lustre of male Formosan *throat.*

Colour-transference. F_1.   Reeves × Versicolor ♂.

Back :   Ruby and purple lustre of male Versicolor *throat and breast.*

Female parent to *male* offspring.

Colour-transference.
Body :   The exact shade of rich brilliant brown found on the 4th, 5th and 6th lateral rectrices of the female Reeves.

Pattern-transference.

Male parent to *female* offspring.

Pattern-transference. F_1.   Reeves × Formosan ♀ " B."

Breast :   *Anterior* feathers pattern of female Formosan *flank.*

Pattern-tranference. F_1.   Reeves × Versicolor ♀ " B."

Breast :   *Posterior* feathers pattern of female Versicolor *anterior* breast feathers.

Female parent to *female* offspring.

Pattern-transference. F_1. Reeves × Formosan ♀ "Y" (1911 male-assuming).

Interscapulars: *Anterior* feathers pattern of male Reeves *posterior* interscapulars, *female* parent to *male* offspring.

Pattern-transference. F_1. Reeves × Formosan ♂.

Tail: Outer vane of lateral rectrix pattern of female Reeves *primary*.

This examination of the plumage of the F_1 sterile hybrids reveals several interesting points.

1. The number of female characters of their species transmitted by the male parents to their female offspring is quite considerable, and the number of male characters of her species transmitted by the female parent to her male offspring is fewer.

2. There are quite an appreciable number of cases of colour and pattern-transference, and three of the colour-transferences were transmitted by the male parent to the male offspring and are of the nature of secondary sexual characters.

3. That in both crosses Reeves × Formosan and Reeves × Versicolor the structure of the posterior back feathers and tail coverts of the males, degenerate in both male parents, has been transmitted normal, like the male of her species to her male offspring by the female parent.

A fourth very remarkable point is the difference between the 1910 plumage of F_1 Reeves × Formosan ♀ "Y," and that of 1911. Much of the 1910 plumage was transmitted by the male parent, many areas being that of the female of his species, whilst the male-assuming plumage of 1911 was, in every area on which it occurred, the male plumage of the female parent species; showing that to this one sterile individual both parents had transmitted characters of the opposite sex of their species absolutely pure to type.

APPENDIX B.

FERTILE HYBRIDS.

Mutating condition of four areas from unpatterned to patterned :

[Throat, Breast, Flank, Thigh-tuft,

in the males of F_1 "*BA*," F_2 "*BBA*," F_3 "*BBBA*" and F_4 "*BBBA*" *inter se* Silver × Swinhoe (Series 1), Fertile Hybrids.]

Throat, Breast, Flank, Thigh-tuft.

F_1. " *BA*," ♂.   Ten months old bird, mutating condition *present* on throat and lateral anterior breast feathers. *Present* on thigh-tuft, colour fulvous.

F_1. " *BA*," ♂, " *E*."   Parent of F_2 *inter se*, 1909, 1910. *Present* on throat and lateral anterior breast feathers. *Absent* on thigh tuft.

Mutation appears on flank and thigh-tuft in F_2.

F_2. " *BBA*," ♂, " *E*."   (Parent of F_3.) *Present* on throat and many lateral and central anterior breast feathers. Mutation present on flank and thigh-tuft.

„   ♂, " *A*."   *Present* on throat and some anterior breast laterals. *Absent* from flank. *Present* on thigh-tuft.

„   ♂, " *B*."   *Present* on a few lateral throat feathers. *Absent* from breast and flank and thigh-tuft.

„   ♂, " *C*."   *Present* on throat and anterior breast and on flank and thigh-tuft.

„   ♂, " *D*."   *Absent* from throat, breast and flank and thigh-tuft.

F_3. " *BBBA*," ♂, " *A*."   *Present* all over throat: *Absent* from breast. *Present* on flank and thigh-tuft.

„   ♂, " *B*."   *Absent* from throat, breast and flank. *Present* on thigh-tuft.

„   ♂, " *C*."   *Present* all over throat and breast. *Present* on flank and thigh-tuft.

„   ♂, " *D*."   *Absent* from throat, breast and flank. *Present* on thigh-tuft.

„   ♂, " *E*."   *Absent* from throat and breast. *Present* on flank and thigh-tuft.

„   ♂, " *F*."   *Present* all over throat and on a few anterior laterals on breast. *Present* on flank and thigh-tuft.

„   ♂, " *G*."   *Present* on throat laterals and anterior breast laterals. *Present* on flank and thigh-tuft.

F_3. "*BBBA*," ♂, "*P.*" Parent of F_4 *inter se*, Si. × Si. × Si. × Sw. (Ring inscription " 13, XI. F_4.")

Mutation increased: throat nearly white, mutation pattern *present* on every breast feather, *present* on flank and thigh-tuft.

F_4. "*BBBA*" *inter se*. Si. × Si. × Si. × Sw. ♂♂.

"*D*," ♂. *Present* all over throat and on every feather in breast and flank. Anterior of breast nearly white. Thigh-tuft very white.

"*H*," ♂. *Present* on every feather, throat, breast and flank in a fine white line. *Present* on thigh-tuft.

"*N*," ♂. *Present* on every feather, throat, breast and flank. Anterior breast nearly white. Pattern on many feathers reduced to a white rachis, vanes black. *Present* on thigh-tuft.

"*L*," ♂. *Present* all over throat, breast, and flank : throat and anterior of breast nearly white, similar to " *D* " ♂. *Present* on thigh-tuft.

"*E*," ♂. *Present* (being bred from 1914 in Pen 7) has the mutation feathers all over throat, breast and flanks in broad pattern like " *D* " and " *L*." *Present* on thigh-tuft.

Males. Series 1.

Mutation from unpatterned to patterned in Males of Series 1.

Thigh-tuft.

The thigh tuft, very conspicuous in the living bird is unpatterned black in the males of both parent species, but is found in " *A* " series in a patterned condition.

Males of both parent species :

Swinhoe ♂ *unpatterned* black.

Silver ♂♂ „ „

" *BA*," F_1. ♂. Ten months bird immature plumage. Mutation, *present patterned* fulvous and black.

" *BA*," F_1. " *A, B, C, D, E*," (*D, E, B, C, A*) ♂♂. Absent: *unpatterned* black as in males of both parent species.

" BBA," F_2.   " D, C, A," ♂ ♂.   *Present*: white pattern on black ground
　　　　　　and black pattern on white ground.

" BBA," F_2.   " E, B," ♂ ♂.   *Absent*: unpatterned black as in males of
　　　　　　both parent species.

" BBBA," F_3.   " P, B, D, A, G, C[1], F, E."   *Present*: white pattern
　　　　　　on black ground and black pattern on white ground.

" BBBA " *inter se*, F_4.   " L, H, D, N, E."   *Present*: white pattern on
　　　　　　black ground and black pattern on white ground.

An investigation into the origin of this mutation in the thigh-tuft
led to comparison with the female Swinhoe breast and flank patterns
and showed these to be the undoubted source of the vandyke designs of
the thigh-tuft mutations which cause quite as marked a change in the
appearance of the birds as do the mutations of throat, breast and flank.
Individual birds differ as to the amount of white on the mutated
plumage of the thigh-tuft.

The transition plumage of the immature male Silver on breast and
flank was also examined, but the design is a rounded form, not the
pointed vandyke which characterises the " A " series thigh-tuft and the
female Swinhoe breast and flank.

Mutation of central rectrices from unpatterned to patterned condition.

Males of parent species :

　　　　Swinhoe unpatterned white, rachis white.
　　　　Silver ♂ ♂ (2).
　　　　One unpatterned white.   Rachis black for two inches from
　　　　　　quill end.
　　　　One with very slight pattern near the quill end.   Rachis
　　　　　　black for half the length of feather from quill end.

" BA," F_1.   " A, B, C, D, E," ♂ ♂.   Both vanes heavily patterned.

" BBA," F_2.   " A, B. C, D, E," ♂ ♂.   Outer vanes much patterned.

" BBBA," F_3.   " C," ♂.   *Unpatterned white, rachis white* (Swinhoe).

　　" 　　 F_3.   " F," ♂.   Patterned white : rachis black at quill end
　　　　　　changing to white.

　　" 　　 F_3.   " D," ♂.   Slightly patterned white : rachis black at
　　　　　　quill end.

　　" 　　 F_3.   " A," ♂.   *Unpatterned white*: rachis black at quill end
　　　　　　(Silver).

---

[1] Much white and one feather the exact pattern of female Swinhoe breast feather.

"*BBBA*," F_3. "*B*," ♂. Patterned white: rachis black from quill end, two-thirds of length.

„ F_3. "*E*," ♂. Slightly patterned white: rachis black at quill end.

„ F_3. "*G*," ♂. Patterned white: *rachis white*.

„ F_3. "*P*," ♂. Patterned white: *rachis white*.

"*BBBA*" *inter se*, F_4. "*H*," ♂. Patterned the whole length of the feather. Rachis black from quill to half the length.

„ „ F_4. "*N*," ♂. Unpatterned white. Rachis black for three inches at quill end.

„ „ F_4. "*D*," ♂. Patterned throughout length of feather. Rachis black for two-thirds of length from quill.

„ „ F_4. "*L*," ♂. Heavily patterned quill to tip on outer vanes, slightly patterned on inner vanes. Rachis dark throughout from quill to tip.

Note. F_3. "*C*," ♂, has the central rectrix pure Swinhoe type. It is observed also in this bird that one thigh-tuft feather was the exact pattern of the female Swinhoe breast.

It is evident that as amongst the female Silvers, so also amongst the male Silvers considerable diversity of pattern exists in the central rectrices, but it is equally evident that in F_4 *inter se* we have a hybrid or mutating condition in which there is evidence of the working of Mendel's law.

DESCRIPTION OF PLATES.

(All figures are natural size unless the contrary is stated.)

STERILE HYBRIDS.

PLATE XXXIV.

Tail coverts.

Transmission of structure by female parent to male offspring:

Fig. 1. *P. formosanus* ♂.

Fig. 2. *P. reevesi* ♂.

Fig. 3. *P. versicolor* ♂.

Fig. 4. F_1 (Reevesi ♀ × Formosanus ♂) ♂.

Transmission of pattern by male parent to female offspring :

Fig.   5.   *P. formosanus* ♀ .
Fig.   6.   *P. reevesi* ♀ .
Fig.   7. F_1 (Reevesi ♀ × Versicolor ♂) ♀ " *B.* "
Fig.   8. F_1 (Reevesi ♀ × Formosanus ♂) ♀ " *B.* "
Fig.   9. F_1 (Reevesi ♀ × Formosanus ♂) ♀ " *Y.* "
Fig.   10. F_1 (Reevesi ♀ × Versicolor ♂) ♂ .

PLATE XXXV.

Back feathers.

Transmission of structure by female parent to male offspring :

Fig.   1.   *P. formosanus* ♂ (degenerate barbs).
Fig.   2. F_1 (Reevesi ♀ × Formosanus ♂) ♂ .
Fig.   3.   *P. reevesi* ♂ (normal barbs).
Fig.   4. F_1 (Reevesi ♀ × Versicolor ♂) ♂ .
Fig.   5.   *P. versicolor* ♂ (degenerate barbs).

Transmission of pattern by male parent to female offspring :

Fig.   6.   *P. formosanus* ♀ .
Fig.   7. F_1 (Reevesi ♀ × Formosanus ♂) ♀ .
Fig.   8.   *P. reevesi* ♀ .
Fig.   9. F_1 (Reevesi × Versicolor) ♀ " *B.* "
Fig.   10.   *P. versicolor* ♀ .

PLATE XXXVI.

Scapulars.

Fig.   1.   *P. formosanus* ♂ .
Fig.   2.   *P. formosanus* ♀ .
Fig.   3.   *P. reevesi* ♂ .
Fig.   4.   *P. reevesi* ♀ .
Fig.   5.   *P. versicolor* ♂ .
Fig.   6.   *P. versicolor* ♀ .
Fig.   7. F_1 (Reevesi ♀ × Formosanus ♂) ♂ .
Fig.   8. F_1 (Reevesi ♀ × Formosanus ♂) ♀ .
Fig.   9. F_1 (Reevesi ♀ × Versicolor ♂) ♂ .
Fig.   10. F_1 (Reevesi ♀ × Versicolor ♂) ♀ .

PLATE XXXVII.

Interscapulars.

Fig.   1.   *P. reevesi* ♀ .
Fig.   2.   ,,   ,,
Fig.   3.   *P. versicolor* ♀ .
Fig.   4.   ,,   ,,
Fig.   5.   *P. reevesi* ♂ .
Fig.   6.   ,,   ,,
Fig.   7.   *P. versicolor* ♂ .
Fig.   8.   ,,   ,,

PLATE XXXVIII.

Interscapulars.

PLATE XXXIX.

Lateral Rectrices.

FERTILE HYBRIDS.

PLATE XL.

Throat, Breast and Flank.

PLATE XLI.

Interscapulars.

PLATE XLII.

Throat, Breast and Flank.

[1] For the nature of the birds denoted by the different letters in Plates XL—L the reader is referred to Series No. 1 of the pedigrees on p. 248.

PLATE XLIII.

Throat, Breast and Flank.

J. F_2.   Male.
N. F_3.   Male.

PLATE XLIV.

Throat, Breast and Flank.

X. F_4.   Male.
Z. F_4.   Male.

PLATE XLV.

Primaries.

A.   Male Swinhoe.
B.   Male Silver.

PLATE XLVI.

Primaries.

E. F_1.   Male.
K. F_2.   Male.

PLATE XLVII.

Primaries.

C. F_3.   Male.
Q. F_3.   Male.

PLATE XLVIII.

Primaries.

Y. F_4.   Male.
Z. F_4.   Male.

PLATE XLIX.

Thigh-tuft.

A.   Male Swinhoe.
B.   Male Silver.
C. F_1.   Male (immature, 10 months old).
E. F_1.   Male.

PLATE L.

Thigh-tuft.

K. F_2.   Male.
R. F_3.   Male.
X. F_4.   Male.
Z. F_4.   Male.

1

2

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PLATE XXXIV

3

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PLATE XXXV

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PLATE XXXVI

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PLATE XXXVII

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PLATE XXXVIII

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PLATE XXXIX

-⅗" nat size
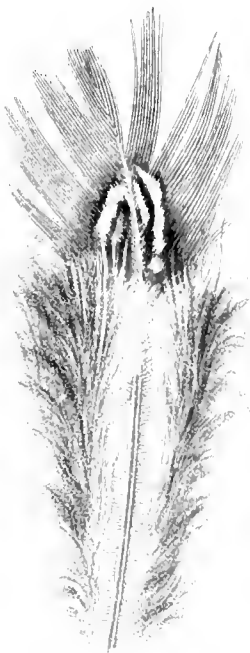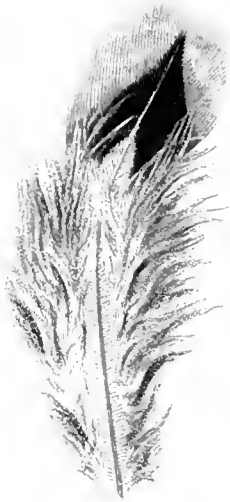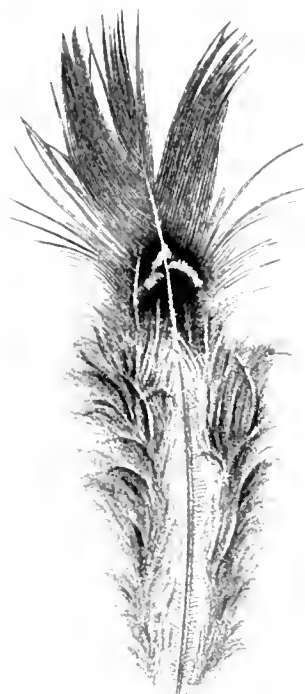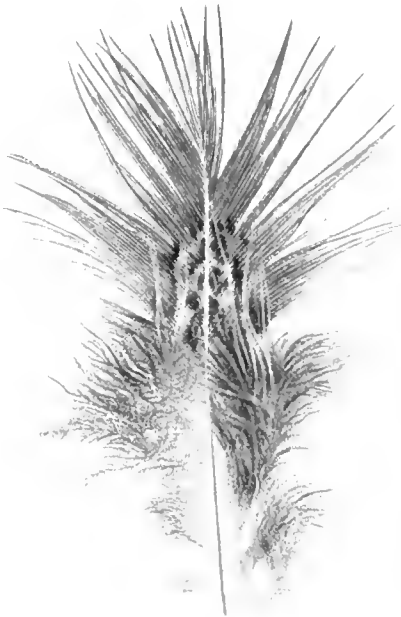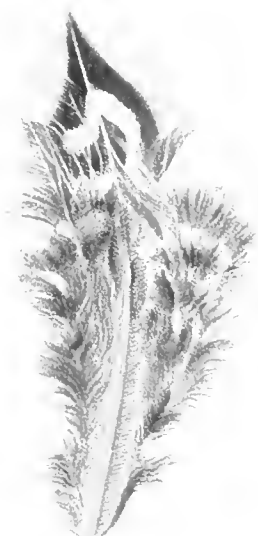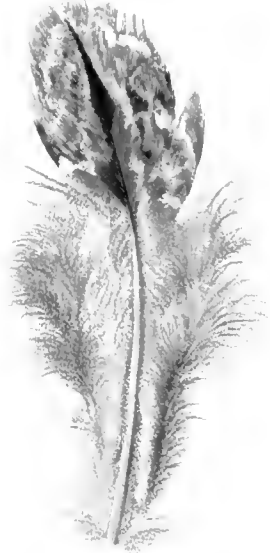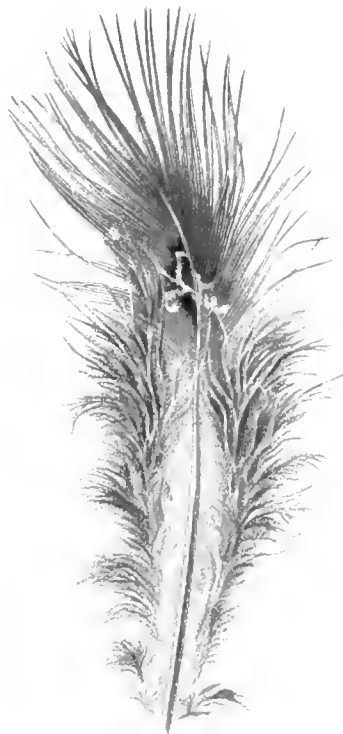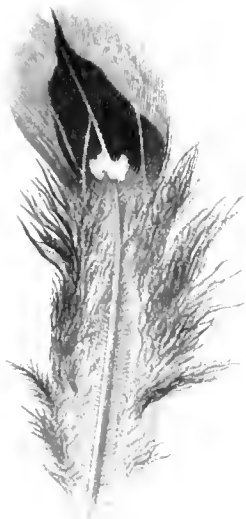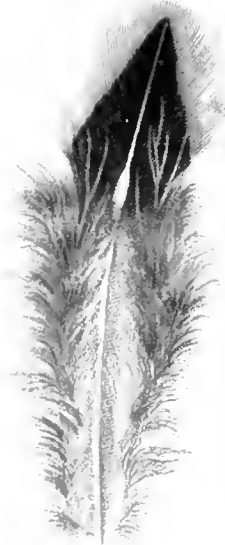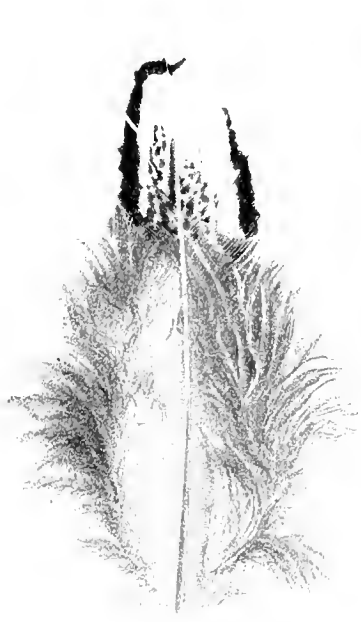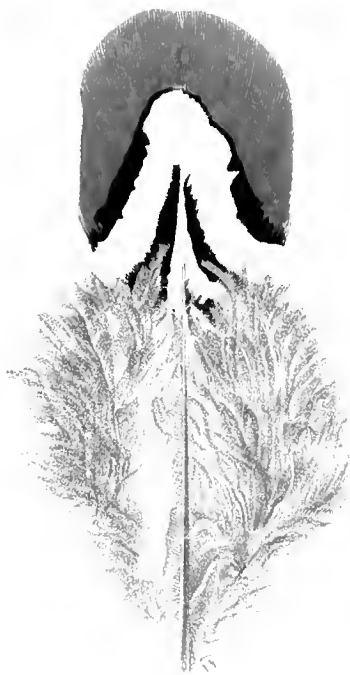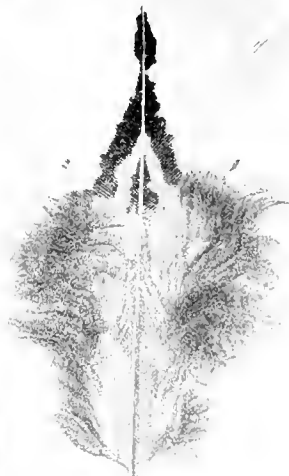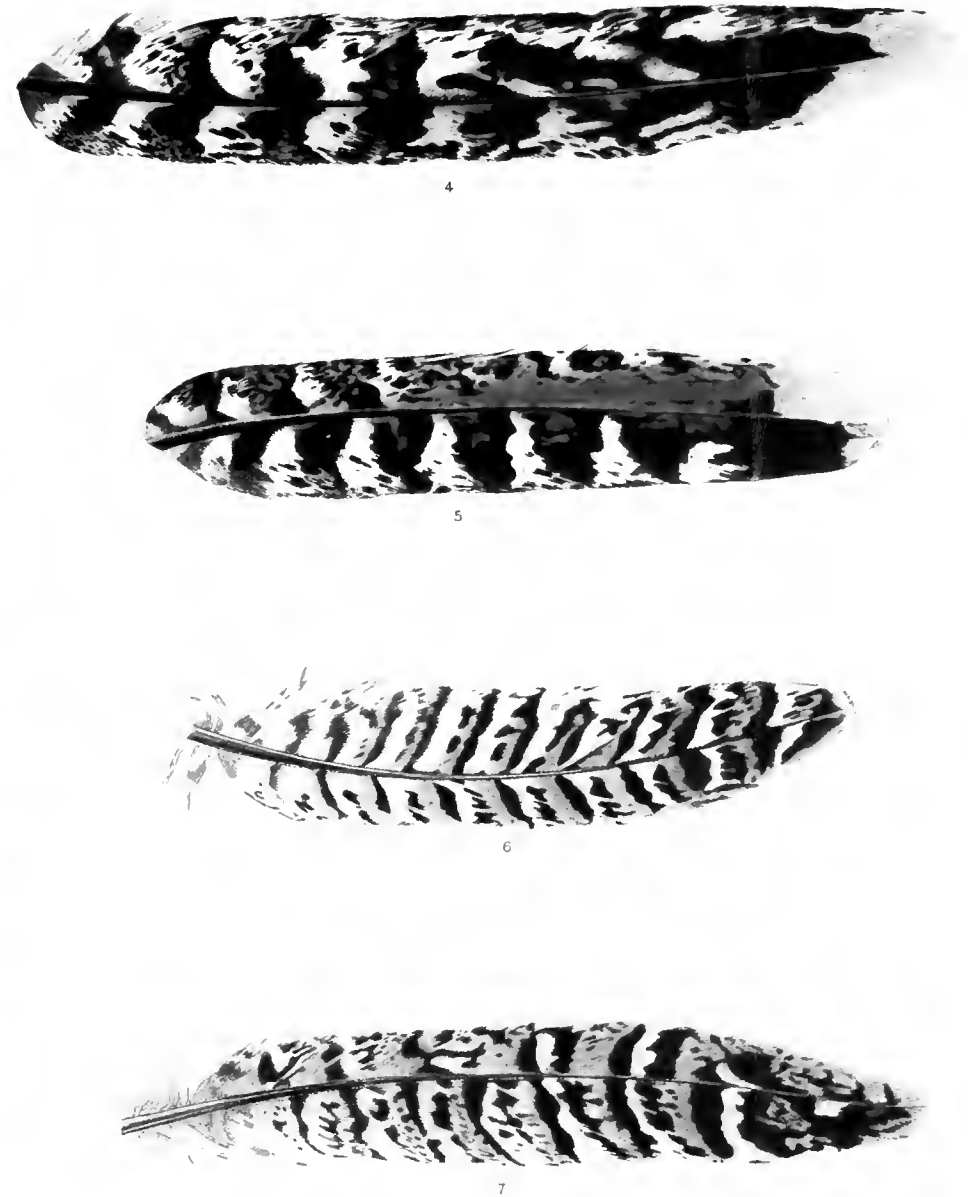
A

B

Throat, Breast and Flank.

PLATE XLI

A

Interscapulars.

C

E

Throat, Breast and Flank.

J

N
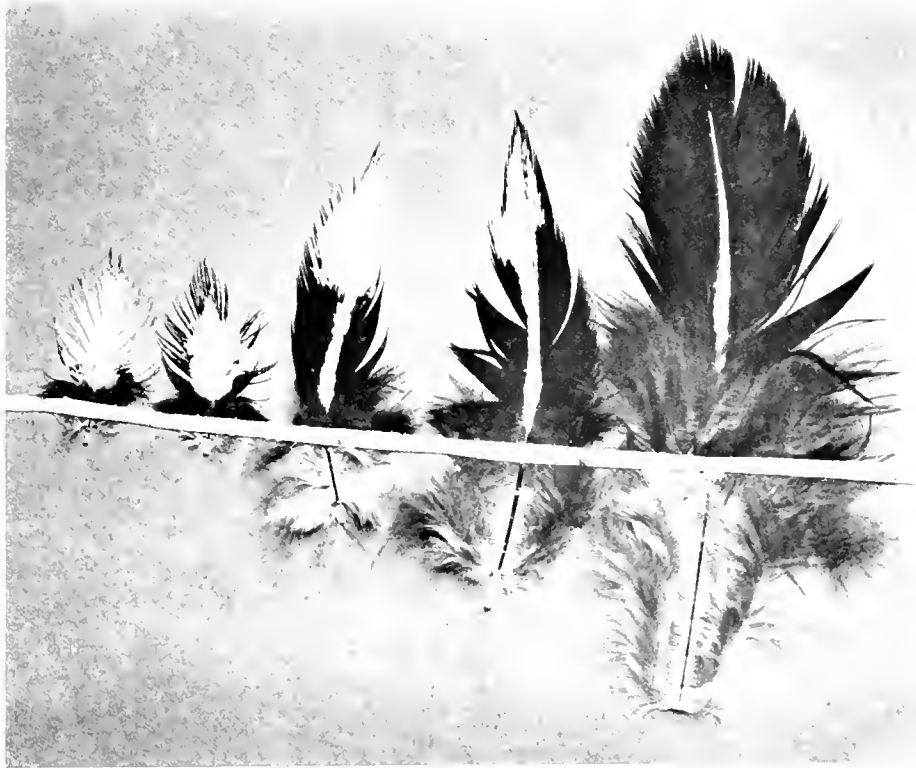
Throat, Breast and Flank.

X

Z

Throat, Breast and Flank.

A　　　　　　　　　　　　　　　　　　　B

Primaries.
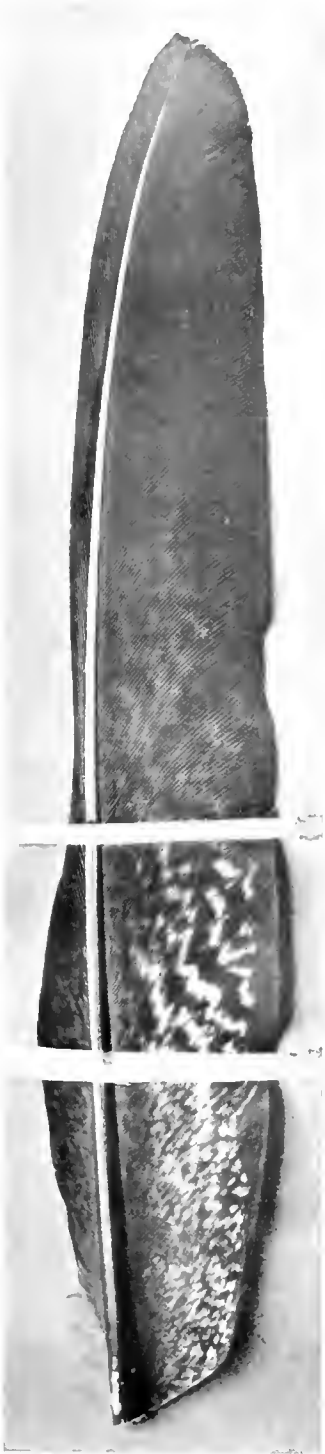
E   K

Primaries.

C   Q

Primaries.

Y   Z

Primaries.

A

B

C

E

Thigh-tuft.

PLATE L
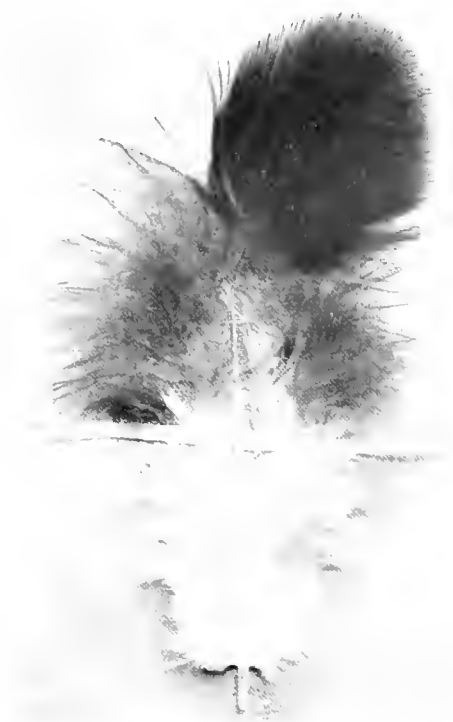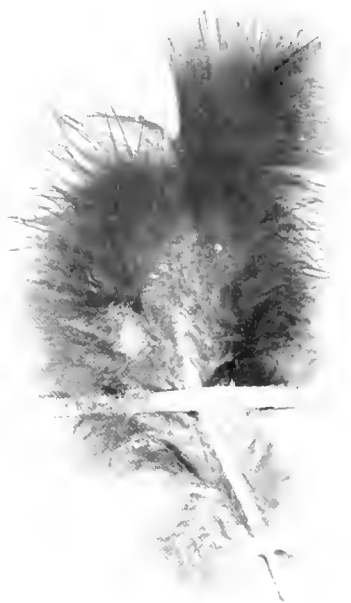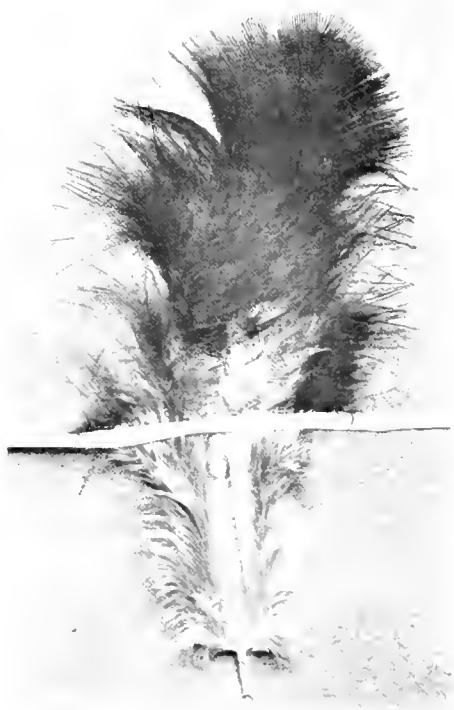
K
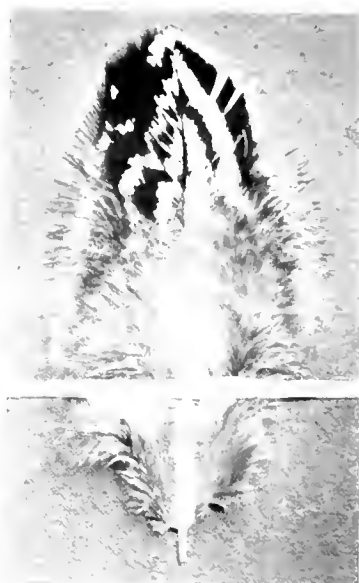
R

X
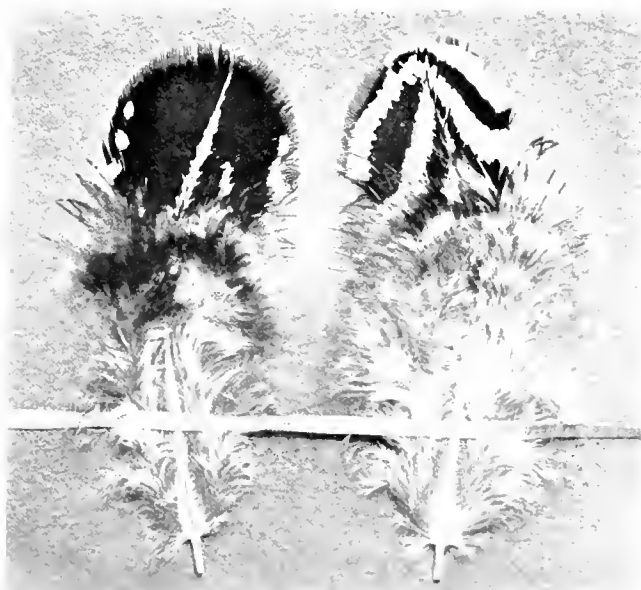
Z

Thigh-tuft.

A CRITICISM OF THE HYPOTHESIS OF *LINKAGE* AND *CROSSING OVER*.

By A. H. TROW, D.Sc., F.L.S.

THE publication of *The Mechanism of Mendelian Heredity* by Morgan, Sturtevant, Muller, and Bridges, marks a definite stage in the development of the hypothesis of *linkage* and *crossing over*. The authors' faith in this hypothesis has evidently become so strong that they are not unlikely to infect others with their belief, irrespective of any real demonstration of its validity. It seems therefore desirable that the hypothesis should be subjected to independent criticism. Such criticism is really rendered necessary by the fact that although the authors devote much time and space in their book to the elucidation of the simple Mendelian ratios, they give no clear coherent account of their mode of explanation of the more complex and troublesome ratios which students of genetics classify under the headings *coupling, repulsion, reduplication*, and *crossing over*.

Drosophila ampelophila, the type which these authors have mainly investigated, appears to be an organism admirably suited to genetic analysis. Already more than a hundred factors have been isolated and their relationships studied in some detail. The authors may be congratulated on their choice of such excellent material, and on the skill and industry with which they are exploiting it. One peculiarity of the organism deserves special mention—the x or n number of chromosomes is four, and the set is remarkable in that one of them is spherical in form, the remaining three being rod-like.

In the study of the hundred factors already recognised in this organism, many deviations from the normal gametic and zygotic ratios have been recognised, and it is these which have apparently led the authors (who reject the reduplication hypothesis) to elaborate their alternative hypothesis of linkage and crossing over.

They interpret the normal Mendelian ratios as due to the presence of the factors in different chromosomes. Thus if two factors A and B give the zygotic ratio of $9:3:3:1$, they interpret this by locating A and B in different chromosomes. It is obvious that if these factors *really* are in different chromosomes, there *can be* no linkage and crossing over, in Morgan's sense, so far as they are concerned. It appears, moreover, from their statements, although the actual evidence is not directly produced in sufficient amount to form a proof, that many factors are linked together in such a way that they behave during the segregation period as an indivisible whole. For example, X, Y, Z may represent characters which are generally completely correlated. Tested separately by crossing with the corresponding recessive, x, y, z, we should find that
$$\left.\begin{array}{l} X : x \\ Y : y \\ Z : z \end{array}\right\} :: 3 : 1,$$
but, and this is the vital point, generally, though not always, $XYZ : xyz :: 3 : 1$. Such a behaviour is well described as *linkage*, and would be undiscoverable if it were really absolute. Its discovery only becomes possible when the linkage can be broken down. The genesis of the hypothesis of crossing over is no doubt traceable to the fact that the linkage is not absolute, except in rare cases.

Perhaps the most essential element in the crossing over hypothesis is the conception of the factors as being represented by the chromomeres of the chromosomes, as if indeed they were numbered beads on a string, each having a definite locus of its own. The factors are not only restricted to a special chromosome, but to a special position in this. So much is this the case that the authors have represented in the Frontispiece of their book the position of no fewer than thirty-six factors: in one chromosome alone the positions of as many as nineteen are shown.

The authors take their standpoint (confessedly or by implication) on the following grounds :

(1) that the individuality of the chromosomes may be now accepted as fully established,

(2) that rod-like chromosomes actually occur in *Drosophila*,

(3) that in the prophases of meiosis in certain organisms whose cytology has been more fully studied than that of *Drosophila*, the homologous chromosomes may be observed in the positions required by the hypothesis,

(4) that the percentage of cross-overs obviously! depends upon the distance apart of the factors concerned, and therefore, conversely,

(5) that the percentage of cross-overs enables one to allocate the factors concerned to their proper relative positions.

Let us consider whether the authors' standpoint is a safe one. We may admit the validity of the contention that the chromosomes have an individuality of their own, and that the relations of the chromomeres to each other remain approximately constant—to do otherwise would render all further discussion futile.

We may admit too that in *Drosophila* crossed chromosomes probably occur in meiosis. It should be added that the crossing over hypothesis renders the detailed cytological study of these cross-overs in this organism a matter of pressing importance.

Now, do the homologous chromosomes cross according to the laws of chance, anyhow, anywhere, or according to some geometrical scheme ? It is exceedingly difficult to discover whether the authors have really adequately considered this point.

Let us suppose that the cross-over takes place once only, and at the middle point of the chromosome, and let the number of factors (or chromomeres) be reduced to six, and lettered $ABCDEF$ and $abcdef$; the chromosome being regarded as a paired chromosome of a nucleus in meiosis of some F_1 plant. We should get the following arrangement:
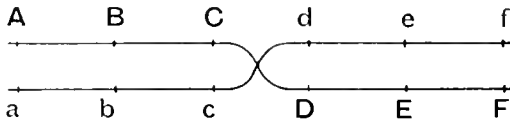
Crossing over takes place so as to produce the cross-overs

$$Ad, \ Ae, \ \mathbf{Af}; \quad Bd, \ Be, \ Bf; \quad Cd, \ Ce, \ Cf$$

$$aD, \ aE, \ aF; \quad bD, \ bE, \ bF; \quad cD, \ cE, \ cF$$

in equal numbers, and the non-cross-overs

$$AB, \ AC, \ BC; \quad ab, \ ac, \ bc$$

$$DE, \ DF, \ EF; \quad de, \ df, \ ef$$

in equal numbers.

Put in another way, any one of the capital letters *A*, *B*, *C* combines with any one of the small letters *d*, *e*, *f*, and any one of the small letters *a*, *b*, *c* combines with any one of the large letters *D*, *E*, *F* to form *crossovers*, but there are *no corresponding non-cross-overs*, if *every chromosome has a constant behaviour*. If however for every chromosome which crosses over in this definite way, another similar chromosome in another nucleus does not cross over at all, so that the ♂ and ♀ contributions in this case simply separate from each other, then there would be non-cross-overs present, *AD*, *AE*, *AF*; etc. (along with others) corresponding to the set of cross-overs given above. We should get, if both types occur equally often, equal numbers of cross-overs and non-cross-overs, e.g.,

AD   ad   aD   Ad

non-cross-overs   cross-overs

50 %   50 %

If two, three, or four chromosomes remained uncrossed for each one that crosses, the percentage of cross-overs would fall to 33 %, 25 %, 20 %, and so on. In such a scheme it is obvious that the percentage of cross-overs does not give any information as to the relative position of the factors in the chromosomes. This behaviour does not depend on the selection of the middle point as the locus of the actual crossing over. If the crossing over takes place at *any one fixed point*, a similar conclusion is inevitable. Hence we may be sure that the authors of the crossing over hypothesis had some other scheme than this in view.

Now if the crossing over does not take place (if it takes place at all) always at the middle part of the chromosome, or some other definite point, let us suppose that it takes place according to the laws of chance at *any one* point. With the same chromosomes as before, with six factors each, there will obviously be five points at which crossing over will take place, as in the following figures:
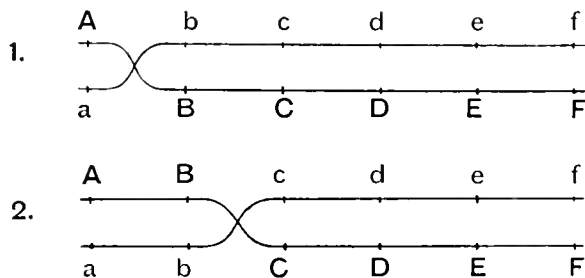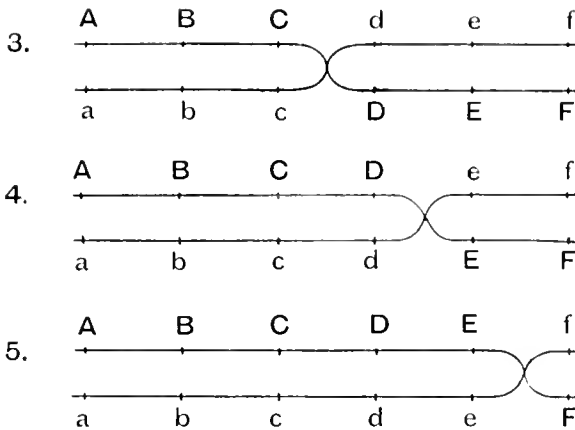
From these figures we can see that the cross-overs in which *A* is concerned are as follows:

1.	*Ab*	*Ac*	*Ad*	*Ae*	*Af*
2.		*Ac*	*Ad*	*Ae*	*Af*
3.			*Ad*	*Ae*	*Af*
4.				*Ae*	*Af*
5.					*Af*

In all five cases	1*Ab*	2*Ac*	3*Ad*	4*Ae*	5*Af*
Similarly with B.		1*Bc*	2*Bd*	3*Be*	4*Bf*
C.			1*Cd*	2*Ce*	3*Cf*
D.				1*De*	2*Df*
and E.					1*Ef*

According to this scheme the cross-overs appear to occur in numbers exactly proportional to the distance apart of the factors concerned. For example, *F* is five units from *A*, *D* three units, and *B* one unit. *Af* occurs five times, and *Ad* three times as often as *Ab*. This is not exactly obvious until it has been worked out, but my mathematical colleagues agree with me that it is perfectly true. This is doubtless the mathematical basis upon which the hypothesis of the localization of the factors has been built up. We have however to note that the essence of the scheme consists in determining the ratio between cross-overs and non-cross-overs. An examination of the figures will show that we get the following relationships:

$$\frac{Ab}{AB} = \frac{1 \text{ cross-over}}{4 \text{ non-cross-overs}} = \begin{cases} 20 \ / \ \text{of} \\ \text{cross-overs} \end{cases} \qquad \frac{Bc}{BC} = \frac{1 \text{ C. O.}}{4 \text{ N. C. O.}} = \begin{cases} 20 \ / \ \text{of} \\ \text{cross-overs} \end{cases}$$

$$\frac{Ac}{AC} = \frac{2 \text{ cross-overs}}{3 \text{ non-cross-overs}} = 40 \ / \qquad \frac{Bd}{BD} = \frac{2 \text{ C. O.}}{3 \text{ N. C. O.}} = 40 \ /$$

$$\frac{Ad}{AD} = \frac{3 \text{ C. O.}}{2 \text{ N. C. O.}} = 60 \ / \qquad \frac{Be}{BE} = \frac{3 \text{ C. O.}}{2 \text{ N. C. O.}} = 60 \ /$$

$$\frac{Ae}{AE} = \frac{4 \text{ C. O.}}{1 \text{ N. C. O.}} = 80 \ / \qquad \frac{Bf}{BF} = \frac{4 \text{ C. O.}}{1 \text{ N. C. O.}} = 80 \ /$$

$$\frac{Af}{AF} = \frac{5 \text{ C. O.}}{0 \text{ N. C. O.}} = 100 \ /$$

$$\frac{Cd}{CD} = \frac{1 \text{ C. O.}}{4 \text{ N. C. O.}} = 20 \ / \qquad \frac{De}{DE} = \frac{1 \text{ C. O.}}{4 \text{ N. C. O.}} = 20 \ /$$

$$\frac{Ce}{CE} = \frac{2 \text{ C. O.}}{3 \text{ N. C. O.}} = 40 \ / \qquad \frac{Df}{DF} = \frac{2 \text{ C. O.}}{3 \text{ N. C. O.}} = 40 \ /$$

$$\frac{Cf}{CF} = \frac{3 \text{ C. O.}}{2 \text{ N. C. O.}} = 60 \qquad \frac{Ef}{EF} = \frac{1 \text{ C. O.}}{4 \text{ N. C. O.}} = 20 \ /$$

If we assume that a single chromosome may have twenty-six factors arranged in a row, $A \ldots Z$, then

$$\frac{Ab}{AB} = \frac{1 \text{ C. O.}}{24 \text{ N. C. O.}} \qquad \frac{Az}{AZ} = \frac{25 \text{ C. O.}}{0 \text{ N. C. O.}}$$

The cross-overs in which A alone is concerned would range from 4 / to 100 /. In general we may say then that cross-overs and non-cross-overs would occur in this scheme, and that while the number of cross-overs increases with the distance apart, the number of non-cross-overs decreases. The percentage of cross-overs however is always proportional to the distance apart of the respective factors. If in addition to the chromosomes whose behaviour is traced in this scheme, there are other chromosomes which do not cross, the percentages of cross-overs become of course reduced, but nevertheless still remain exactly proportional to the distances apart of the factors.

This scheme, without further elaboration, appears at first sight to substantiate the crossing over hypothesis, and one is somewhat surprised to find that it has not been worked out in detail by Morgan himself.

Let us note that with n factors we get the following general formula for the series traced above:

$$\frac{1\ \text{C. O.}}{(n-2)\ \text{N. C. O.}}, \quad \frac{2\ \text{C. O.}}{(n-3)\ \text{N. C. O.}}, \quad \frac{3\ \text{C. O.}}{(n-4)\ \text{N. C. O.}}, \cdots \frac{(n-1)\ \text{C. O.}}{(n-n)\ \text{N. C. O.}}.$$

The percentages of cross-overs become, using the formulae

$$\frac{Ab \times 100}{AB + Ab}, \quad \frac{Ac \times 100}{AC + Ac}, \quad \text{etc.}$$

$$\frac{1 \times 100}{n-1}, \quad \frac{2 \times 100}{n-1}, \quad \frac{3 \times 100}{n-1}, \cdots \frac{(n-1) \times 100}{n-1};$$

a series in arithmetical progression.

If the factors are uniform in size, the least difference between the observed percentages, that between Lethal 1 (·7) and White (1·0), may be regarded as the common difference, and the number of factors may be readily determined, as approximately 300. It is however very noteworthy (even critical for the crossing over hypothesis) that the highest percentage recorded in No. 1 chromosome is 65·5, and that the factors are crowded at one end of the chromosome and quite absent from the other. Why should one end of a chromosome be favoured more than the other? Surely the results should be of such a nature that they may be read from either end. The crowding represents high reduplication. Critical study of numerous cases of high reduplication will probably prove fatal to the Morgan hypothesis.

But a single-cross-over scheme such as this is inadequate to account for all the facts. With a single cross-over taking place by chance at any locus in the chromosome, we get all the combinations which appear in cases of dihybridism, i.e. where two pairs of allelomorphs, such as Aa, Bb, are involved, but we *do not* secure all the combinations which are required in a case of trihybridism, where there is another pair, say Cc. In order that such a combination as AbC should appear, even occasionally, it is necessary that a double cross-over should take place, thus:
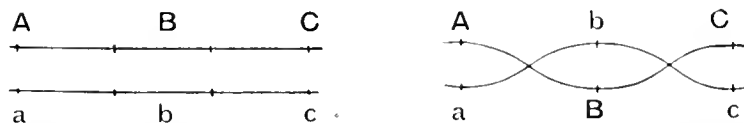
Hence we may deduce the rule that if there are n pairs of segregating allelomorphs, the number of the loci for the crossings-over must be

$n - 1$. If crossing over is common to homozygotes and heterozygotes, as Sturtevant suggests, then the number of crossings over, whether segregation takes place or not should be only one less than the numbers of factors; in other words, there must be a crossing over place between each factor and its neighbours. Every possible assortment of characters is thus provided for.

But it does not seem probable that the law which applies to single cross-overs should apply also to double and multiple cross-overs, and indeed Morgan and his colleagues, in order to explain many remarkable deviations from the law, have already had to resort to three or more subordinate hypotheses, which they discuss in some detail under the heads of (1) differential viability, (2) double or multiple crossing over, (3) interference, and (4) incapacity for crossing over when the Y (male) chromosome is involved; etc.

I have thought it worth while to trace the effect of the addition of another crossing over in the case examined on pp. 284–286. If we take the figures on pp. 284–285 numbered 1 to 4, as a starting point, and confine our attention to those cross-overs in which A is involved, we get the following sets of figures and relations deduced from them.

Double Crossing Over with 6 Factors, **ABCDEF.**
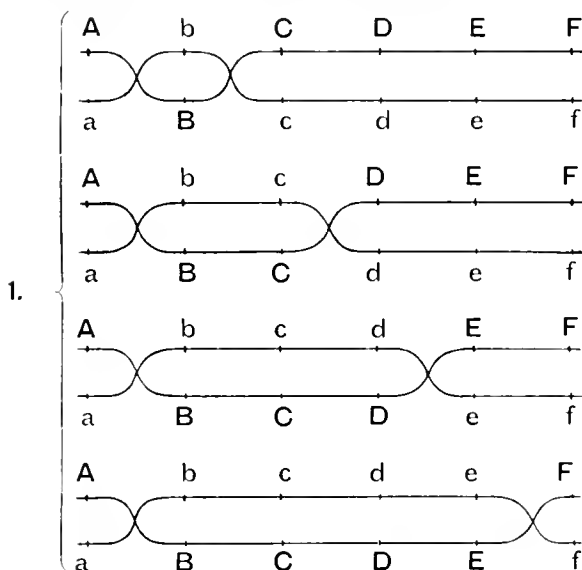
C. O.				N. C. O.			
Ab				*AC*	*AD*	*AE*	*AF*
Ab	*Ac*				*AD*	*AE*	*AF*
Ab	*Ac*	*Ad*				*AE*	*AF*
Ab	*Ac*	*Ad*	*Ae*				*AF*
4*Ab*	3*Ac*	2*Ad*	1*Ae*	1*AC*	2*AD*	3*AE*	4*AF*

2.
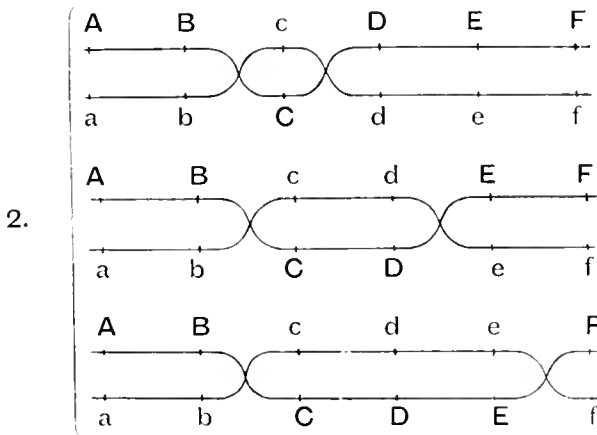
C. O.			N. C. O.				
Ac			*AB*		*AD*	*AE*	*AF*
Ac	*Ad*		*AB*			*AE*	*AF*
Ac	*Ad*	*Ae*	*AB*				*AF*
3*Ac*	2*Ad*	1*Ae*	3*AB*	0*AC*	1*AD*	2*AE*	3*AF*

3.
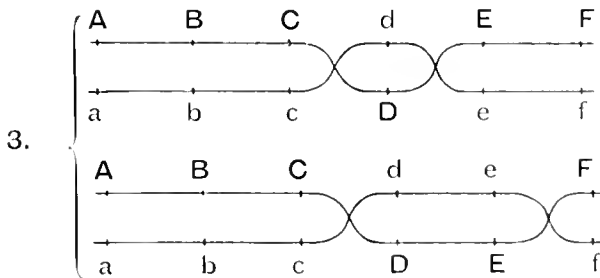
	C. O.			N. C. O.			
Ad		AB	AC		AE	AF
Ad	Ae	AB	AC			AF
$2Ad$	$1Ae$	$2AB$	$2AC$	$0AD$	$1AE$	$2AF$

	C. O.			N. C. O.			
$1Ae$		$1AB$	$1AC$	$1AD$	$0AE$	$1AF$

Hence the sum of these cases will be

	C. O.				N. C. O.				
1.	$4Ab$	$3Ae$	$2Ad$	$1Ae$	$0AB$	$1AC$	$2AD$	$3AE$	$4AF$
2.		$3Ae$	$2Ad$	$1Ae$	$3AB$	$0AC$	$1AD$	$2AE$	$3AF$
3.			$2Ad$	$1Ae$	$2AB$	$2AC$	$0AD$	$1AE$	$2AF$
4.				$1Ae$	$1AB$	$1AC$	$1AD$	$0AE$	$1AF$
	$4Ab$	$6Ae$	$6Ad$	$4Ae$	$6AB$	$4AC$	$4AD$	$6AE$	$10AF$

The percentages of cross-overs become

$$\frac{Ab}{AB} = \frac{4 \text{ C. O.}}{6 \text{ N. C. O.}} = 40 \text{ / of cross-overs}$$

$$\frac{Ac}{AC} = \frac{6 \text{ C. O.}}{4 \text{ N. C. O.}} = 60 \text{ /}$$

$$\frac{Ad}{AD} = \frac{6 \text{ C. O.}}{4 \text{ N. C. O.}} = 60 \text{ /}$$

$$\frac{Ae}{AE} = \frac{4 \text{ C. O.}}{6 \text{ N. C. O.}} = 40 \text{ /}$$

The series of percentages is a symmetrical one, but the terms are not in an arithmetical progression.

If we take twenty-six factors, A to Z, instead of six, A to F, we get the following series:

C. O.

1.	24.Ab	23.Ac	22.Ad	21.Ae	20.Af	19.Ag......1.Ay
2.		23.Ac	22.Ad	21.Ae	20.Af	19.Ag..... 1.Ay
3.			22.Ad	21.Ae	20.Af	19.Ag......1.Ay
4.				21.Ae	20.Af	19.Ag......1.Ay
5.					20.Af	19.Ag......1.Ay
6.						19.Ag......1.Ay
⋮						⋮
24.						1.Ay

The whole series of cross-overs in this case will be

24.Ab	46.Ac	66.Ad	84.Ae	100.Af	114.Ag
126.Ah	136.Ai	144.Aj	150.Ak	154.Al	156.Am
156.An	154.Ao	150.Ap	144.Aq	136.Ar	126.As
114.At	100.Au	84.Av	66.Aw	46.Ax	24.Ay

The number of N. C. O.'s is readily determined from the table on p. 292. The ratios $\left(\dfrac{\text{C. O.}}{\text{N. C. O.}}\right)$ are thus determinable in any case of double crossing over, and can be compared with the corresponding ratios for a single crossing over. (See Table on p. 293.)

Thus, with twenty-six factors, A to Z, a number approximating to those already located in the first chromosome, it is not difficult to calculate the corresponding series of ratios and the percentages by this method. The table on p. 293 gives the result of such a calculation arranged to show the relationships of *single* and *double crossing-over*.

My mathematical colleague, Prof. Pinkerton, has suggested to me the following formulae, as a ready means of calculating the values of the ratio, $\dfrac{\text{C. O.} \times 100}{\text{C. O.} + \text{N. C. O.}}$.

Let there be n pairs of allelomorphs, Aa, Bb, Cc, etc., numbered from 1 to r and on to n, thus:

$$1 \quad 2 \quad \ldots\ldots\ldots r \ldots\ldots \quad n$$
$$A \quad B \ldots\ldots\ldots M \ldots\ldots\ldots$$
$$a \quad b \ldots \quad \ldots m \ldots\ldots\ldots$$

The following formulae enable one to calculate the number of C. O.'s **Am**, etc., with little difficulty.

One crossing : $r - 1$.

Two crossings : $(r-1)(n-r)$.

Three crossings : $(r-1)\dfrac{(n-r)(n-r-1)}{1 \cdot 2} - \dfrac{(r-1)(r-2)(r-3)}{1 \cdot 2 \cdot 3}$.

Four crossings: $(r-1)\dfrac{(n-r)\,(n-r-1)\,(n-r-2)}{1\times2\times3} + \dfrac{(r-1)\,(r-2)\,(r-3)}{1\times2\times3}(n-r)$.

Five crossings: $(r-1)\dfrac{(n-r)\ldots(n-r-3)}{1\times2\times3\times4}$

$$+\dfrac{(r-1)\,(r-2)\,(r-3)}{1\times2\times3}\times\dfrac{(n-r)\,(n-r-1)}{1\times2} + \dfrac{(r-1)\,(r-2)\,(r-3)\,(r-4)\,(r-5)}{1\times2\cdot3\times4\times5}.$$

The following formulae give the numbers of C. O.'s + N. C. O.'s.

One crossing: $n-1$.

Two crossings: $\dfrac{(n-1)\,(n-2)}{1\times2}$.

Three crossings: $\dfrac{(n-1)\,(n-2)\,(n-3)}{1\times2\times3}$. Etc.

Non-Cross-Overs.

AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ
0	1	2	3	4	5	6	7	8	9	10	11	12	13	11	15	16	17	18	19	20	21	22	23	24
23	0	1	2	3	4	5	6	7	8	9	10	11	12	13	11	15	16	17	18	19	20	21	22	23
22	22	0	1	2	3	1	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
21	21	21	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
20	20	20	20	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
19	19	19	19	19	0	1	2	3	4	5	6	7	8	9	10	11	12	13	11	15	16	17	18	19
18	18	18	18	18	18	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
17	17	17	17	17	17	17	0	1	2	3	1	5	6	7	8	9	10	11	12	13	14	15	16	17
16	16	16	16	16	16	16	16	0	1	2	3	1	5	6	7	8	9	10	11	12	13	14	15	16
15	15	15	15	15	15	15	15	15	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
14	11	14	14	14	11	14	14	11	11	0	1	2	3	4	5	6	7	8	9	10	11	12	13	11
13	13	13	13	13	13	13	13	13	13	0	1	2	3	1	5	6	7	8	9	10	11	12	13	
12	12	12	12	12	12	12	12	12	12	12	12	0	1	2	3	1	5	6	7	8	9	10	11	12
11	11	11	11	11	11	11	11	11	11	11	11	11	0	1	2	3	4	5	6	7	8	9	10	11
10	10	10	10	10	10	10	10	10	10	10	10	10	10	0	1	2	3	4	5	6	7	8	9	10
9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	1	2	3	1	5	6	7	8	9
8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	0	1	2	3	4	5	6	7	8
7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	0	1	2	3	4	5	6	7
6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	0	1	2	3	4	5	6
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	0	1	2	3	4	5
4	4	4	4	4	1	4	4	4	4	1	1	4	4	1	4	4	4	4	1	0	1	2	3	4
3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	0	1	2	3
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	1	2
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1

	Double Crossing Over Per cent.	Single Crossing Over Per cent.
Ab / AB	$\dfrac{24}{276} = 8\cdot0$	$\dfrac{1}{21} = 4\cdot0$
Ac / AC	$\dfrac{46}{254} = 15\cdot3$	$\dfrac{2}{23} = 8\cdot0$
Ad / AD	$\dfrac{66}{234} = 22\cdot0$	$\dfrac{3}{22} = 12\cdot0$
Ae / AE	$\dfrac{84}{216} = 28\cdot0$	$\dfrac{4}{21} = 16\cdot0$
Af / AF	$\dfrac{100}{200} = 33\cdot3$	$\dfrac{5}{20} = 20\cdot0$
Ag / AG	$\dfrac{114}{186} = 38\cdot0$	$\dfrac{6}{19} = 24\cdot0$
Ah / AH	$\dfrac{126}{174} = 42\cdot0$	$\dfrac{7}{18} = 28\cdot0$
Ai / AI	$\dfrac{136}{164} = 45\cdot3$	$\dfrac{8}{17} = 32\cdot0$
Aj / AJ	$\dfrac{144}{156} = 48\cdot0$	$\dfrac{9}{16} = 36\cdot0$
Ak / AK	$\dfrac{150}{150} = 50\cdot0$	$\dfrac{10}{15} = 40\cdot0$
Al / AL	$\dfrac{154}{146} = 51\cdot3$	$\dfrac{11}{14} = 44\cdot0$
Am / AM	$\dfrac{156}{144} = 52\cdot0$	$\dfrac{12}{13} = 48\cdot0$
An / AN	$\dfrac{156}{144} = 52\cdot0$	$\dfrac{13}{12} = 52\cdot0$
Ao / AO	$\dfrac{154}{146} = 51\cdot3$	$\dfrac{14}{11} = 56\cdot0$
Ap / AP	$\dfrac{150}{150} = 50\cdot0$	$\dfrac{15}{10} = 60\cdot0$
Aq / AQ	$\dfrac{144}{156} = 48\cdot0$	$\dfrac{16}{9} = 64\cdot0$
Ar / AR	$\dfrac{136}{164} = 45\cdot3$	$\dfrac{17}{8} = 68\cdot0$
As / AS	$\dfrac{126}{174} = 42\cdot0$	$\dfrac{18}{7} = 72\cdot0$
At / AT	$\dfrac{114}{186} = 38\cdot0$	$\dfrac{19}{6} = 76\cdot0$
Au / AU	$\dfrac{100}{200} = 33\cdot3$	$\dfrac{20}{5} = 80\cdot0$
Av / AV	$\dfrac{84}{216} = 28\cdot0$	$\dfrac{21}{4} = 84\cdot0$
Aw / AW	$\dfrac{66}{234} = 22\cdot0$	$\dfrac{22}{3} = 88\cdot0$
Ax / AX	$\dfrac{46}{254} = 15\cdot3$	$\dfrac{23}{2} = 92\cdot0$
Ay / AY	$\dfrac{24}{276} = 8\cdot0$	$\dfrac{24}{1} = 96\cdot0$
Az / AZ	$\dfrac{0}{300}$	$\dfrac{25}{0} = 100\cdot0$

The maximum number of cross-overs in double crossing over occurs between A on the one hand, and M and N on the other. The number of cross-overs is no longer proportional to the distance apart of the factors. Y is twenty-four times the distance of B from A, but the cross-overs Ab and Ay are equal in number. C is twice as far from A as B is, yet $\dfrac{Ac}{Ab} = \dfrac{15\cdot3}{8\cdot0}$, i.e., is less than 2.

Now these two systems of crossing over obviously cannot occur together in the same chromosome and the same nucleus. The gametes consequently owe their constitution to the operation of one or the other scheme (not to both). The observed ratios can only be adequately interpreted if we know the relative frequency of the divisions which occur in each of these two systems. The American authors appear to have adopted the following point of view. If three pairs of factors are concerned, Bb, Ee, Nn, it is necessary, that all kinds of assortments should be obtained, that three types of behaviour should be possible to the chromosomes, as represented in the following diagram.
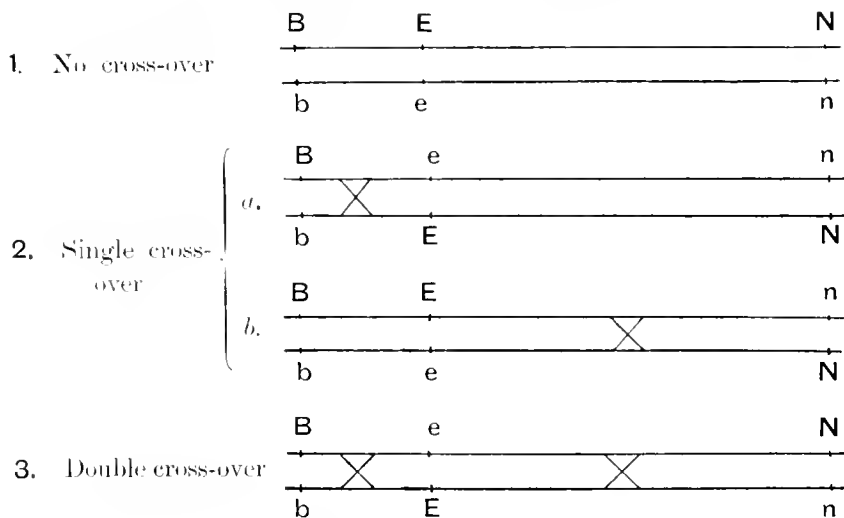
By experiment, the eight types of gametes postulated are actually found, as well as the *numbers in which they occur*, and those individuals whose constitution corresponds to the hypothetical double cross-over are always fewer in number than those of any of the other classes.

These three types of behaviour appear to be independent of each other, as by hypothesis, they take place in different nuclei. I think

therefore it would be an error to try and shew the possible mathematical relations which may exist between them. The frequency of a double cross-over can perhaps be calculated, like a double event, from the frequency of the corresponding single cross-overs, but it is extremely doubtful whether we are justified in assuming any mathematical relationship between a no cross-over (whole distance) and a single cross-over (part distance). But the numbers of the gametes alone, even were such mathematically related to each other, would not suffice to enable us to calculate the error of the ratio $\dfrac{\text{C. O.}}{\text{N. C. O.}}$ due to the presence of double crossing over. We should require to know at least the *total number of the factors* located in the chromosome as well.

But there are greater difficulties involved in the hypothesis. We have seen that there must be as many crossing over places as there are known factors, less one. By hypothesis, these factors are not recognisable unless they are separable in the process of crossing over. Hence we can fairly assume that multiple crossing over must be frequent; if the F_1 plant is heterozygotic for the twenty-six factors A to Z, there must be twenty-five crossing over places, and the chromosome would sometimes appear as a closely wound spiral, thus:
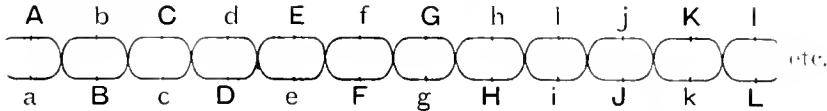
In such a scheme as this, with the maximum of crossing over, there are cross-overs and non-cross-overs in abundance, but for each type of cross-over, there is no corresponding non-cross-over. Crossing over is absolute, i.e. 100 , for

$$\frac{Ab}{AB} = \frac{Ad}{AD} \cdots \frac{Az}{AZ} = \frac{1 \ \text{C. O.}}{0 \ \text{N. C. O.}}.$$

Every alternate factor, too, appears to be absolutely correlated; there is no crossing over at all in Morgan's sense.

It can be shewn that for each type of crossing over—simple, double, triple, etc.—there is a different system of ratios; and as a number of these systems must be in operation in any one experiment, whether recorded or not, it is practically impossible to find the true percentage of cross-overs due to a single crossing over by deducting those C. O.'s and N. C. O.'s which are due to multiple crossing over. All that we can say positively is, that double crossing over as compared with single

crossing over, increases the percentage of C. O.'s up to the middle point of the chromosome, and decreases it from that point to the end.

The accurate location of the factors in the chromosomes by means of the empirical determination of the ratio $\dfrac{\text{C. O.}}{\text{N. C. O.}}$ appears therefore to be impossible. At best an approximation only can be secured, as the correction for multiple crossing over is, at any rate, in the present state of our knowledge, unascertainable.

The difficulties due to differential viability may also be practically insurmountable. Interference, or the hindrance to free crossing over caused by the proximity of the factors, cannot be effective in a case of single crossing over. In multiple crossing over, however, such hindrances may certainly occur. A theoretical estimate of them is impossible until we have at our disposal additional data such as the dimensions of the chromosomes and chromomeres at the actual moment of crossing over. In the figure on p. 295, there appears to be a maximum of interference. Crossing over is absolute between the first and second, interference is absolute between the first and third factors.

The crossing over hypothesis, simple enough at first sight, is in reality beset with extraordinary difficulties.

1. Two cardinal points of the hypothesis are: (*a*) that the distance apart of the factors is only directly determinable when two pairs of allelomorphs are alone involved, and (*b*) that the complete assortment of factors is impossible unless there are as many crossings-over (and schemes) as the factors, less one. As the crossing over is supposed to occur indiscriminately in homozygotes and heterozygotes, the actual ratios found can seldom have a simple relation to the pairs of allelomorphs whose behaviour is actually recorded. The disturbing effect of the remaining pairs must always be allowed for. It is perhaps impossible to arrange an experiment in which the F_1 individual is heterozygotic for two pairs of allelomorphs only.

2. When the number of pairs of allelomorphs is reduced to three—*Aa*, *Bb*, and *Cc*—and all other disturbing features of the hypothesis are set aside, a condition, which in practice is perhaps unattainable, we have to note that, by hypothesis, four kinds of behaviour are traceable to the same chromosome:

(*a*) *no crossing over*, when one of the homologous chromosomes is the *Y* chromosome. Most of the experimental data are based on this hypothetical behaviour.

(b) *no crossing over*
(c) *single crossing over* $\Big\}$ when the *Y* chromosome is excluded.
(d) *double crossing over*

Why should a chromosome behave differently as in *b*, *c*, and *d*, or indeed in all four cases? Surely, the cells concerned, and their nuclei, are for all practical purposes indistinguishable from each other.

3. There is a logical fallacy underlying the whole of the crossing over hypothesis, as applied to the location of the factors. Let it be granted that under certain limited conditions the number of cross-overs is proportional to the distance of the factors from each other. It does not follow that the distance of the factors from each other is proportional to the number of the cross-overs. It may be true that "all men are fools"; it does not follow from this that "all fools are men."

In truth, the foundation on which the hypothesis of crossing over has been built up appears to be very unstable. Ruptures and recombinations take place without any adequate cause. Why should a chromosome break where it crosses another? If it break, why not remain broken? If it recombine, what regulates the recombination? What force secures the absence of crossing over where the *Y* chromosome is concerned? What determines the constant numerical relation between the no-ruptures, single ruptures, and double ruptures?

Finally, let it be noted that the graphic representation of the location of the factors is a type of representation common to every set of phenomena which can be expressed as percentages. The exponents of the reduplication hypothesis may very well accept the plans of the chromosomes, as graphic representations of the relative strengths of reduplication. For their purposes the diagrams must be read from the 50 / mark (no reduplication) towards the two ends. 90 is indeed a graphic representation of -10 / (repulsion).

In this analysis it was not thought worth while to pursue in detail other but somewhat petty difficulties, such as the presence of a spherical chromosome, with cross-overs associated with it; the probability of untwisting taking place in metakinesis; the difficulty of demonstrating a rupture and recombination by the existing cytological methods, and so on. It may be noted, however, that *Drosophila* with its few chromosomes, may shew an unusual amount of chromosome isolation and of reduplication (linkage and crossing over). Whatever may be the fate of their ingenious but, I fear, rather overworked hypothesis, students of genetics will continue to welcome the detailed contributions of these American authors.

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